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# The *depressor mandibulae* muscle in Anura

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**It is well known that the diversity in anuran cranial structure is large, observed in the variation of the bone structure and associated muscles. The *depressor mandibulae* is the jaw muscle that opens the mouth and was considered by many authors useful in delimiting anuran groups. However, there is still much controversy on the value of the m. *depressor mandibulae* as a relationship-indicating character. The goal of this project is to explore the morphological diversity of the *depressor mandibulae* muscle among different families of anurans. Specimens including 60 genera of 17 families of Anura were dissected, using traditional techniques of macroanatomy. Fifteen morphological groups can be distinguished within the anuran species analysed. The insertion point demonstrates little variation. The overall pattern of the origin is also quite stable, except for *Hemisus g. guineensis*, *Arthroleptis* and *Breviceps poweri*, which have an unusual anterior branch of m. *depressor mandibulae* coming from the maxilla. The great diversity in shape of the m. *depressor mandibulae* correlates with the plethora of patterns already mentioned for cranial morphology in Anura. However, it is difficult to assign a specific morphology to a given higher taxon. We also found no evidence that variations in the m. *depressor mandibulae* are associated with particular habits.**

## INTRODUCTION

In frogs, the *depressor mandibulae* is the jaw muscle that opens the mouth. It is derived from the hyoid arch and innervated by the facial nerve. It has a variable origin and, in general, it occupies the area between the otic branch of the squamosal, the *anulus tympanicus*, and the dorsal fascia.

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This muscle is one of the most controversial ones in frogs, evidenced by much discussion around its utility as a phylogenetic character (GRIFFITHS, 1963; LIMESES, 1965; STARRETT, 1968; BURTON, 1983*a-b*, 1986; LYNCH, 1993; BURTON & ZWEIFEL, 1995; LA MARCA, 1995; MANZANO, 1996, 1997; HOYOS, 1999). Many of these authors (BURTON, 1983*a-b*; MYERS & FORD, 1986; FORD, 1989; SAVAGE, 1987; FORD & CANNATELLA, 1993) considered that the m. *depressor mandibulae* is useful to delimit anuran groups. Nevertheless, other authors affirmed that the morphology of the m. *depressor mandibulae* does not form consistent patterns with cladistic or phenetic hypotheses (LYNCH, 1993; HOYOS, 1999).

Reviewing pseudid and hylid myology it was found (AM) that the m. *depressor mandibulae* presents a distinctive morphology in pseudids and phyllomedusine frogs. The amount of contradictory discussion led us to undertake a morphological descriptive survey of the m. *depressor mandibulae* among anurans. The goal of this project is to explore the morphological diversity of *depressor mandibulae* muscle among sixteen families of Anura.

## MATERIALS AND METHODS

Two hundred and twenty seven specimens belonging to seventeen families of Anura (60 genera) were dissected under a stereomicroscope (app. 1). The skin was removed from the cervical and cranial regions (both sides) on each specimen, exposing the *depressor mandibulae* and adjacent musculature. When the muscle was divided, we removed the layers from the most superficial to the deepest. Each dissection was described in detail, focusing especially on the sites of origin and insertion, general morphological characteristics, and the relation of the m. *depressor mandibulae* with other structures (bones, blood vessels, nerves and other muscles). In some cases (particularly in small animals), differential staining with iodine solution (BOCK & SHEAR, 1972) was done. Bones and cartilages of some specimens were stained with alizarine red S and Alcian blue 8GX, respectively, as described by WASSERSUG (1976). The terminology used for bone follows TRUEB (1993) and muscle terminology follows DUELLMAN & TRUEB (1985). All the material is deposited in the herpetological collection of the Fundación Miguel Lillo (FML), the herpetological collection of the Centro de Investigaciones y Transferencia de Tecnología a la Producción (DIAM), Universidad del Valle de Cali (Colombia) (UVC) and the African collection of Dr. Raymond Laurent (RL).

We consider that there are three generalized origin points of the *depressor mandibulae* muscle: *anulus tympanicus*, squamosal and/or dorsal facia. When the muscle is divided in two branches, we define the anterior branch as that branch corresponding to the first branch present in a cephalo-caudal axis. When the anterior branch is overlapped by a branch, we define this condition as deep anterior branch, and superficial anterior branch respectively. The posterior one is that branch present behind the anterior branch. When an extra branch is ahead of our anterior branch, we define that using a name related with its origin point. When the muscle is divided in an external branch and an internal branch, we define those as superficial *depressor mandibulae* and deep *depressor mandibulae* respectively.

To improve our understanding we gathered in groups, species that share similar conditions of *depressor mandibulae* muscle in a table (tab. 1), adding schematic drawings – with special reference to the origin points and general morphology, since the insertion points are stable –, and used STARRETT's (1968) nomenclature with our modifications. STARRETT (1968)

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proposed a notation system for the different *depressor mandibulae* morphologies. We used this notation for our patterns (tab. 1) but found that it was necessary to define new states that were not considered by the Starrett system. For example, the morphology of *Hemisus guineensis guineensis* needs new letters (mx) to describe the branch's origin on the maxilla. Where amuscle division into branches is present, it is represented by a dash. There is a limitation of this nomenclature to describe different branch shapes. For example, the same notation is used to symbolize our groups XIIb and XIIc, despite having differences between them. For that reason we used the subindex 1 and 2 respectively.

## RESULTS

### FAMILY DISCOGLOSSIDAE

*Alytes obstetricans* (fig. 1a). – It has a single *depressor mandibulae* muscle that originates from the dorsal fascia (on the upper part of the m. *dorsalis scapulae*) and m. *levator mandibulae posterioris longus*. The m. *depressor mandibulae* is elongated and approximately triangular, and inserts on the articular process of the lower jaw.

### FAMILY PIPIDAE

*Hymenochirus boettgeri camerunensis*. – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal and posterior edge of the *anulus tympanicus*. It is approximately rectangular, short, bulky and wider at the origin. The m. *depressor mandibulae* does not contact the m. *dorsalis scapulae*. It inserts on the articular process of the lower jaw.

*Xenopus laevis*. – It has a single *depressor mandibulae* muscle that originates from the dorsal fascia at the level of the inferior edge of m. *levator mandibulae posterioris longus*, superior edge of the dorsal branch of m. *dorsalis scapulae*, and lateral edge of the m. *romboideus anterior*. The m. *depressor mandibulae* is elongated and approximately triangular, and inserts on the articular process of lower jaw.

### FAMILY BUFONIDAE

*Bufo arenarum*. – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal. It is bulky and approximately fusiform, wider at the origin and is quite apart from the m. *dorsalis scapulae*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

*Bufo granulosus major*. – It has a single *depressor mandibulae* muscle, but with fibers partially dividing at the origin, arranged bundle-like in different directions, imbricating with each other. It is fusiform and narrow, and covers the m. *cucularis* (= *sternocleidomastoideus*). It originates from the posterior edge of the *anulus tympanicus* and posterior end of the otic process of the squamosal. The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

*Bufo paracnemis*. – It has a single *depressor mandibulae* muscle that originates from the otic branch of the squamosal. It is an approximately rectangular and slightly bulky muscle, wider

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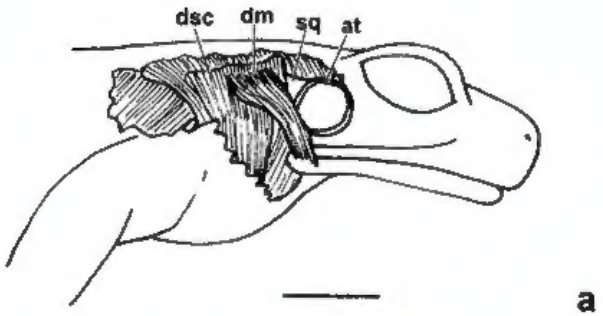


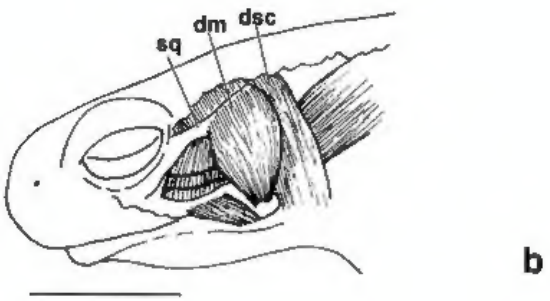


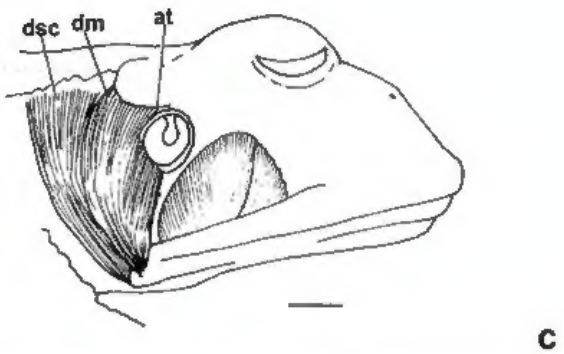


Fig. 1. – (a) *Alytes obstetricans* (FML 02782). Morphology corresponding to group I (tab. 1). Scale bar: 0.5 mm. – (b) *Melanophryniscus rubriventris rubriventris* (FML 02502). Morphology corresponding to group IIb (tab. 1). Scale bar: 0.5 mm. – (c) *Ceratophrys cranwelli* (FML 04924). Morphology corresponding to group IIc (tab. 1). Scale bar: 0.5 mm. – Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dsc, m. *dorsalis scapulae*; sq, squamosal.

Source : MNHN, Paris

at the origin and does not cover the m. *dorsalis scapulae*. It inserts on the articular process of the lower law.

*Bufo spinulosus*. – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal. It is bulky and fusiform, and is formed by bundles of fibers that split easily. It partially covers the m. *cucularis*. The m. *depressor mandibulae* inserts on the articular process of the lower law.

*Melanophryniscus rubriventris rubriventris* (fig. 1b). – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal. It is a fan-shaped and bulky muscle, wide at the origin (the last characteristic only in some specimens) and does not contact the m. *dorsalis scapulae*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

FAMILY LEPTODACTYLIDAE

*Ceratophryinae*

*Ceratophrys cranwelli* (fig 1c). – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal, covered by the *osiculum*, on the posterior border of the *anulus tympanicus* and dorsal fascia (at the level of the m. *dorsalis scapulae*). It is an irregular and thick muscle, wide at the origin and narrow at the insertion. It partially covers the m. *dorsalis scapulae* and inserts on the articular process of the lower jaw.

*Chacophrys pierotti* (fig. 2a). – It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal, the posterior border of the *anulus tympanicus* and dorsal fascia (at the level of the m. *dorsalis scapulae*). It is an irregular muscle, wide at the origin and narrow at the insertion. It partially covers the m. *dorsalis scapulae* and inserts on the articular process of the lower jaw.

*Lepidobatrachus llanensis* (fig. 2b). – It has a single *depressor mandibulae* muscle, fusiform, very thick and long. It originates on the posterior edge of the *anulus tympanicus* and otic process of the squamosal, and inserts on the articular process of the lower jaw.

*Hylodinae*

*Crossodactylus gaudichaudii* (fig. 2c). – It has a thin, short, and fan-shaped *depressor mandibulae* muscle divided into two branches joined at mid-muscle level. Anterior fibers originate on the otic process of the squamosal, and the posterior fibers originate from the dorsal fascia (at the level of the posteromesial edge of the m. *dorsalis scapulae*). The posterior branch is longer than the anterior. It inserts on the articular process of the lower jaw by a short tendon.

*Leptodactylinae*

*Leptodactylus bufonius* (fig. 3a). – It has a wide and approximately triangular *depressor mandibulae* muscle divided into two branches joined at mid-muscle level. The anterior fibers originate from the otic process of the squamosal and posterior fibers from the dorsal fascia (at the level of the mesial edge of the m. *dorsalis scapulae* and m. *latissimus dorsi*). The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

*Leptodactylus chaquensis* (fig. 3b). – It has a single *depressor mandibulae* muscle with a subtle division at its origin. It originates on the otic process of the squamosal and dorsal fascia (at

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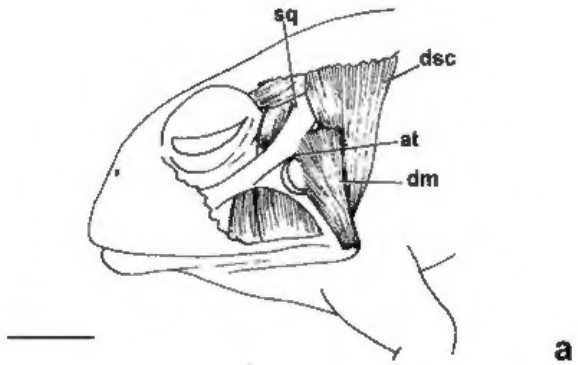


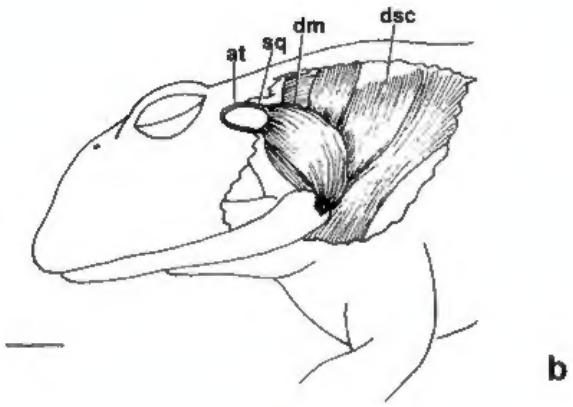


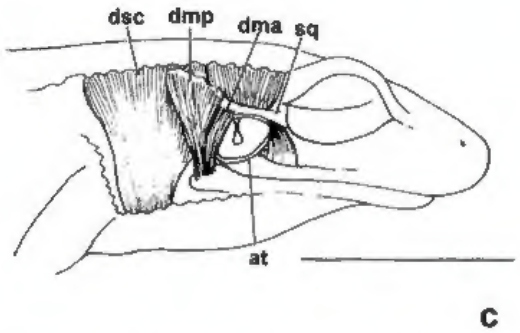


Fig. 2. – (a) *Chacophrys pierotti* (FML 01020). Morphology corresponding to group IIa (tab. 1). Scale bar: 0.5 mm. – (b) *Lepidobatrachus llanensis* (FML 01095). Morphology corresponding to group IIc (tab. 1). Scale bar: 0.5 mm. – (c) *Crossodactylus gaudichaudii* (FML 03497). Morphology corresponding to group III (tab. 1). Scale bar: 0.5 mm. – Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dma, m. *depressor mandibulae anterior*; dmp, m. *depressor mandibulae posterior*; dsc, m. *dorsalis scapulae*; sq, squamosal.

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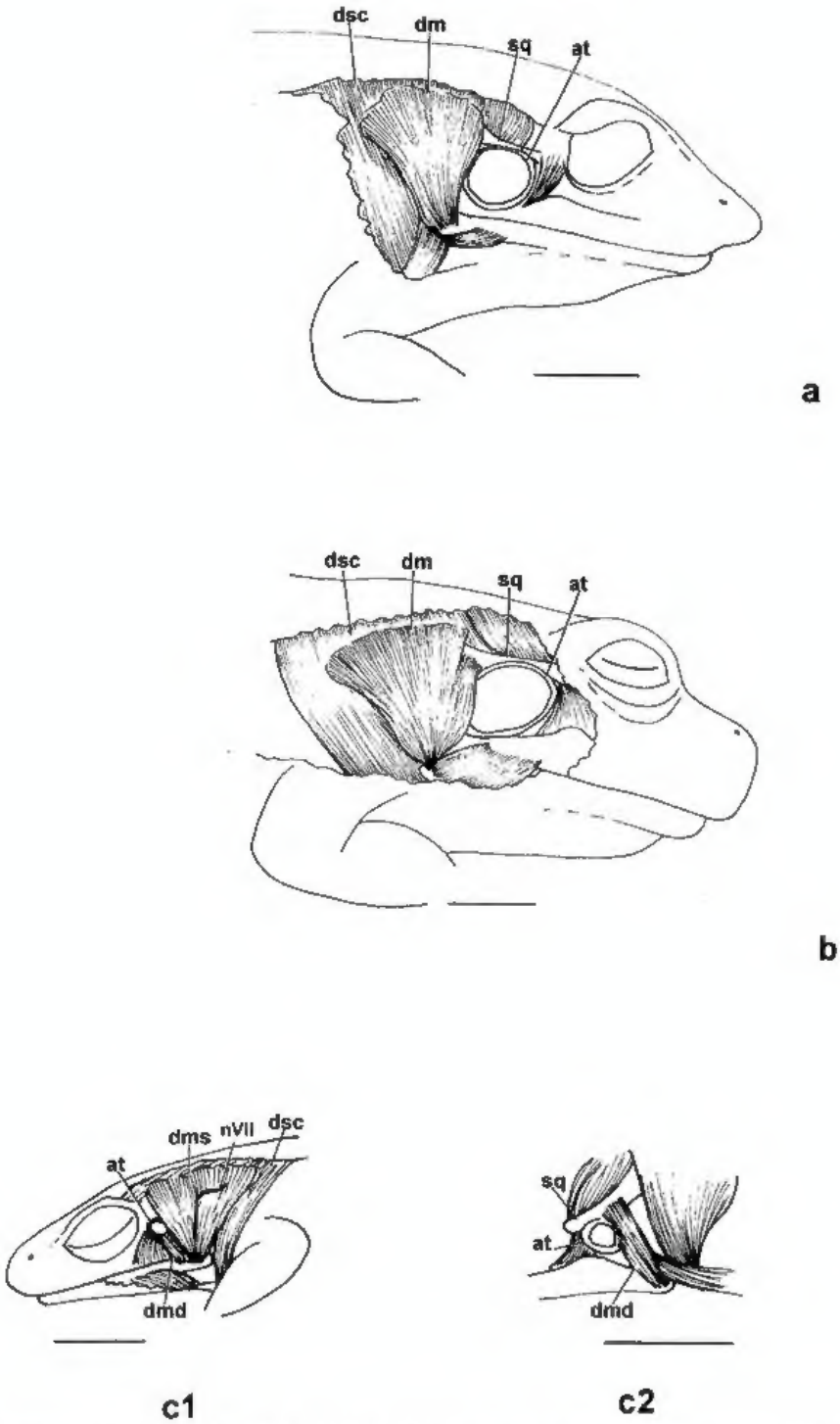


Fig. 3. – (a) *Leptodactylus bufonius* (FML 04642). Morphology corresponding to group III (tab. 1). Scale bar: 0.5 mm. – (b) *Leptodactylus chaquensis* (FML 05490). Morphology corresponding to group III (tab. 1). Scale bar: 0.5 mm. – (c1) *Pseudopaludicola boliviana* (FML 04307). Morphology corresponding to group Vc (tab. 1). Scale bar: 0.2 mm. – (c2) Detail of deep m. *depressor mandibulae* of *P. boliviana*. Scale bar: 0.2 mm. – Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dmd, deep m. *depressor mandibulae*; dms, superficial m. *depressor mandibulae*; dsc, m. *dorsalis scapulae*; nVII, branch of the nerve VII; sq, squamosal.

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the level of mesial edge of the m. *dorsalis scapulae* and m. *latissimus dorsi*). The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

*Pleurodema borellii*. – It has a *depressor mandibulae* muscle divided into two slips, the anterior branch originates from the otic process of the squamosal. It is approximately triangular, wide at the origin. The posterior branch originates from the dorsal fascia (at the level of mesial edge of the m. *dorsalis scapulae* and m. *latissimus dorsi*). It is thicker and wider that the anterior branch. Both branches insert on the articular process of the lower jaw.

*Physalaemus biligonigerus*. – It has a *depressor mandibulae* muscle divided into two branches joined at mid-muscle level. The anterior branch is short and triangular and originates from the otic process of the squamosal. The posterior branch is triangular and wide and originates from the dorsal fascia (at the level of the middle region of the m. *dorsalis scapulae*). Both branches are inserted on the articular process of the lower jaw.

*Pseudopaludicola boliviana* (fig. 3c). – It has a *depressor mandibulae* muscle divided into two slips. A large and fan-shaped superficial slip arises from the dorsal fascia (at the level of the cervical muscles, partially covering the m. *levator scapulae*). This slip is very wide and thin at the origin, and it extends extensively on the dorsal region of the trunk. It covers the posterior part of the *anulus tympanicus* without adhering to it. A nerve V branch passes through the superficial slip. An approximately rectangular, flat and small deep slip originates on the otic process of the squamosal (with some anterior fibers contacting the posterior edge of the *anulus tympanicus*). It contacts the m. *cucularis* at the origin, partially covering it. Both branches of the m. *depressor mandibulae* insert on the articular process of the lower jaw.

*Telmatobiinae*

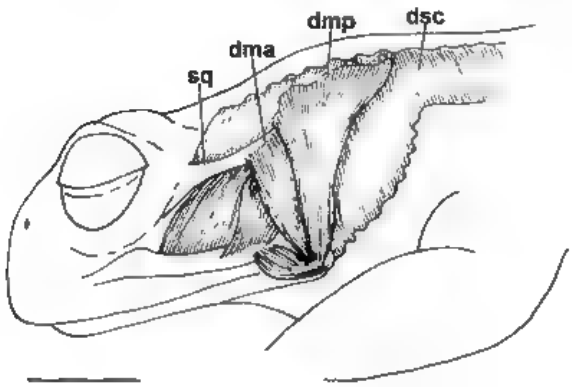
*Alsodes* sp. – It has a *depressor mandibulae* muscle divided into two slips. A thick and rectangular anterior slip originates from the otic process of the squamosal, and a posterior slip that originates from the dorsal fascia (at the level of the middle region of m. *dorsalis scapulae*). The posterior slip is longer than the anterior. Both branches insert on the posterior end of the articular process of the lower jaw.

*Batrachyla* sp. – It has a *depressor mandibulae* muscle divided into two slips. An approximately rectangular, short, and thick anterior slip originates from the otic process of the squamosal. The posterior slip, approximately triangular, long, and thin, originates from the dorsal fascia (at the level of the middle region of the m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

*Hylorina sylvatica*. – It has a *depressor mandibulae* muscle divided into two equally long slips. The anterior slip is thick and rectangular and arises from the otic process of the squamosal. The posterior one, triangular and thicker than the anterior, originates from the dorsal fascia (at the level of the middle region of m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

*Telmatobius laticeps* (fig. 4a). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip is approximately rectangular, narrow, and thick. It originates on the otic process of the squamosal. The posterior slip, approximately triangular and wide at the origin, arises from the dorsal fascia (at the level of the middle region of m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

Source : MNHN, Paris

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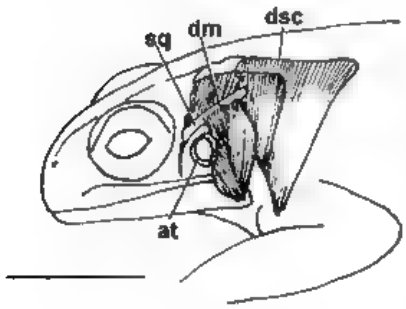


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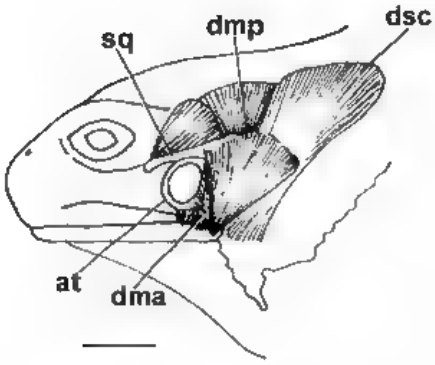



c

Fig 4 (a) *Telmatobius latirostris* (FML 03960) Morphology corresponding to group X (tab. 1) Scale bar 0 5 mm (b) *Crinia georgiana* (DIAM 015) Morphology corresponding to group IIc (tab 1) Scale bar 0 5 mm (c) *Limnodynastes fletcheri* (DIAM 009) Morphology corresponding to group Va (tab 1) Scale bar 0 5 mm Abbreviations at, *anulus tympanicus*, dm, m *depressor mandibulae*, dma, m *depressor mandibulae anterior*, dmp, m *depressor mandibulae posterior*, dsc, m *dorsalis scapulae*, sq squamosal

Source : MNHN, Paris

*Telmatobius serocchii* It has a *depressor mandibulae* muscle divided into two slips. The anterior slip is approximately triangular, narrow, short and thick It arises from the otic process of the squamosal. The posterior slip originates from the dorsal fascia (at the level of the middle region of the m *dorsalis scapulae* and the most anterior fibers at the level of the otoccipital). It is triangular, longer, and twice as thick as the anterior slip. Both branches insert on the articular process of the lower jaw.

*Telmatobius oxycephalus*. It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately triangular and narrow, originates from the otic process of the squamosal The posterior slip, triangular, wide, and longer than the anterior, originates from the dorsal fascia (at the level of the middle region of the m *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

FAMILY MYOBATRACHIDAE

*Myobatrachinae*

*Crinia georgiana* (fig. 4b). – It has a bulky and fusiform single *depressor mandibulae* muscle. It arises from the otic process of the squamosal and the posterior edge of the *anulus tympanicus*, partially covering it The m *depressor mandibulae* does not cover the m. *dorsalis scapulae* There are two kinds of fibers, anterior fibers parallel to the posterior edge of the *anulus tympanicus*, and posterior fibers oriented perpendicular to anterior ones. The m. *depressor mandibulae* inserts on the posterior edge of the lower jaw by a tendon.

*Taudactylus diurnus* It has a fan-shaped single *depressor mandibulae* muscle, wide at its origin Some anterior fibers originate from the otic process of the squamosal Posterior fibers arise from the dorsal fascia (at the level of the anteromesial edge of m. *dorsalis scapulae*). The m. *depressor mandibulae* inserts on the articular process of the lower jaw by a short and thick tendon

*Uperoleia aspera* It has a long and bulky single *depressor mandibulae* muscle, partially covering the tympanum It originates on the dorsal fascia (at the level of the occipital and otic process of the squamosal); the anterior fibers are partially divided originating on the posterodorsal edge of the *anulus tympanicus*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw by a short tendon.

*Uperoleia borealis* It has a *depressor mandibulae* muscle divided into two slips. An anterior slip originates on the posterior edge of the *anulus tympanicus*. This slip is flat and approximately rectangular, and is partially covered by the posterior slip. The posterior slip originates on the external surface of the otic process of the squamosal and the dorsal fascia It is approximately triangular, wider at the origin and does not contact the m *dorsalis scapulae* Both branches insert on the articular process of the lower jaw

*Limnodynastinae*

*Limnodynastes dumerili*. It has a *depressor mandibulae* muscle divided into two slips. An anterior and approximately rectangular slip originates on the ventral edge of the *anulus tympanicus* and otic process of the squamosal, partially covered by the posterior branch The

Source : MNHN, Paris

posterior slip originates on the dorsal fascia, partially covering the m. *dorsalis scapulae*. It is wide and approximately triangular, slightly curved at the origin, surrounding the middle anterior edge of m. *dorsalis scapulae* Both branches insert on the articular process of the lower jaw.

*Limnodynastes convexiusculus* It has a *depressor mandibulae* muscle divided into two slips. An anterior slip originates on the posteroventral edge of the *anulus tympanicus*. It is approximately quadrangular, very short, thin, and narrow. The posterior slip is narrow, elongated and has a noticeable curve caudad. It originates on the dorsal fascia (at the level of the anterior edge of the suprascapula, partially covering the m. *dorsalis scapulae*) Both branches insert on the articular process of the lower jaw.

*Limnodynastes dorsalis* It has a *depressor mandibulae* muscle divided into two slips. An anterior slip, very thin and short, originates on the posterior edge of the *anulus tympanicus*. The posterior slip is fan-shaped and very wide that originates from the dorsal fascia (at the level of the medial edge of m. *dorsalis scapulae* and the otic process of the squamosal). It partially covers the anterior branch. Both branches insert on the articular process of the lower jaw by a tendon.

*Limnodynastes fletcheri* (fig. 4c) It has a *depressor mandibulae* muscle divided into two slips. An anterior approximately triangular, very thin, and short slip originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the mesial edge of the m. *dorsalis scapulae*) and the otic process of the squamosal It is fan-shaped and wide at the origin, and partially covers the anterior branch Both branches insert on the articular process of the lower jaw.

*Limnodynastes ornatus*. It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately rectangular and very short, originates on the posterior edge of the *anulus tympanicus*. The posterior slip is fan-shaped and wide at the origin and originates from the dorsal fascia (at the level of the mesial edge of the m. *dorsalis scapulae* and the otic process of the squamosal). It partially covers the anterior branch. Both branches insert on the articular process of the lower jaw.

*Notaden melanoscaphus* (fig. 5a) It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately rectangular, long and narrow, originates from the otic process of the squamosal The posterior slip originates on the dorsal fascia (at the level of the origin of the m *dorsalis scapulae*) It is approximately rectangular and longer than the anterior slip and is very narrow and curved, crossing over middle part of the m *cucularis* Both branches insert on the articular process of the lower jaw.

*Notaden nichollsi*. It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately fusiform and long, originates on the otic process of the squamosal. The posterior slip originates on the dorsal fascia (at the level of the origin of the m. *dorsalis scapulae*). It is approximately rectangular and longer than the anterior slip, very narrow and curved. Both branches insert on the articular process of the lower jaw.

FAMILY RHINODERMATIDAE

*Rhinoderma darwinii* (fig 5b) It has a single *depressor mandibulae* muscle, approximately triangular and wide at the origin It contacts the anterior border of the m *dorsalis scapulae*

Source : MNHN, Paris

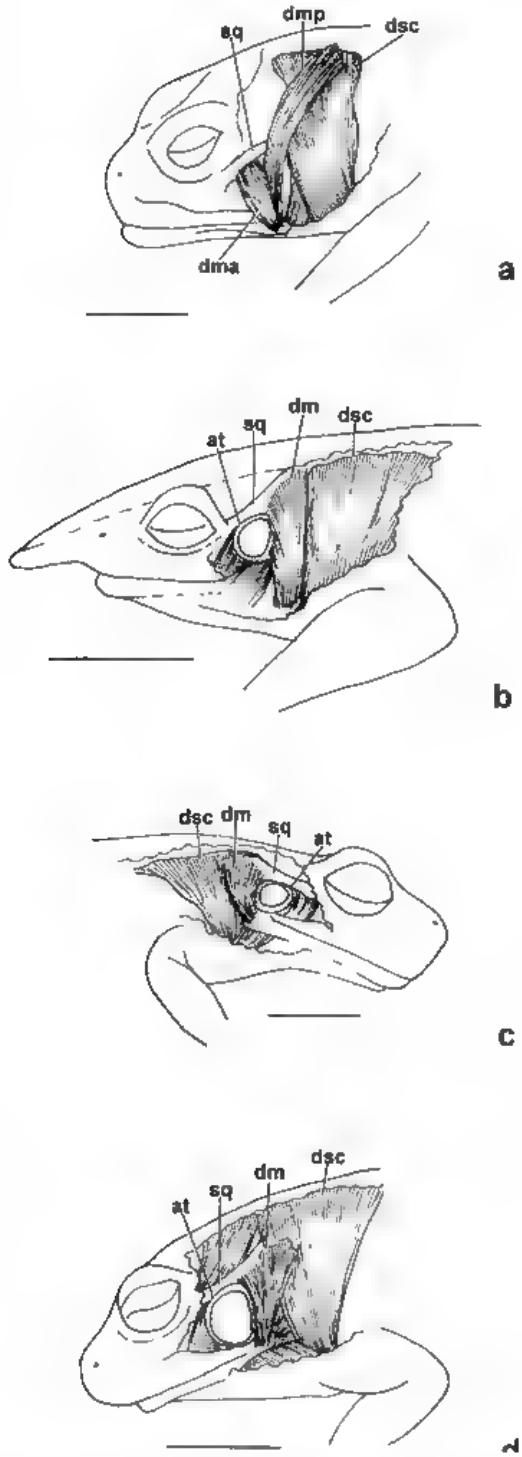



Fig. 5 (a) *Notaden melanoscaphus* (FML 03783) Morphology corresponding to group IX (tab. 1) Scale bar 0 5 mm (b) *Rhinoderma darwinii* (FML 03694) Morphology corresponding to group VIIa (tab. 1) Scale bar 0 5 mm (c) *Gastrotheca christiani* (FML 02117) Morphology corresponding to group IV (tab. 1) Scale bar 0 5 mm (d) *Gastrotheca gracilis* (FML 01769) Morphology corresponding to group IV (tab. 1) Scale bar 0 5 mm Abbreviations at, *anulus tympanicus*, dm, m *depressor mandibulae* dm, m *depressor mandibulae*, dma, m *depressor mandibulae anterior*, dmp, m *depressor mandibulae posterior*; dsc, m *dorsalis scapulae*; sq, squamosal

Source : MNHN, Paris

It has anterior fibers originating on the posterior edge of the *anulus tympanicus* The posterior fibers originate from the posterior end of the otic process of the squamosal. The m. *depressor mandibulae* inserts on the articular process of the lower jaw

FAMILY HYLIDAE

*Hemiphractinae*

*Gastrotheca christiani* (fig. 5c) It has a single *depressor mandibulae* muscle that originates from the dorsal fascia, the otic process of the squamosal, and the posterior edge of the *anulus tympanicus* Approximately rectangular and wide at the origin, it contacts with the anterior border of the m. *dorsalis scapulae*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw

*Gastrotheca chrysosticta* It has a single *depressor mandibulae* muscle that originates from the dorsal fascia, the otic process of the squamosal, and the posterior edge of the *anulus tympanicus* Approximately rectangular, wide at the origin, it contacts the anterior border of the m. *dorsalis scapulae*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

*Gastrotheca gracilis* (fig. 5d). – It has a single *depressor mandibulae* muscle that originates from the dorsal fascia, the otic process of the squamosal, and the posterior edge of the *anulus tympanicus*. Approximately triangular and wide at the origin, the muscle contacts the anterior border of the m. *dorsalis scapulae*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

*Hylinae*

*Acris crepitans* (fig. 6a). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately triangular and elongated, originates on the otic process of the squamosal, and partially covers the posterior edge of the *anulus tympanicus*. The posterior slip, very narrow, thin, and curved, originates on the dorsal fascia (at the level of the middle part of m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

*Argenteohyla siemersii*. It has a *depressor mandibulae* muscle divided into three slips. The anterior slip, approximately rectangular and narrow, originates on the posterior edge of the *anulus tympanicus*. The middle slip, approximately rectangular and wide at the origin (longer than anterior slip), originates on the posterior edge of otic process of the squamosal. The posterior slip, triangular and wide (longer than middle slip), originates on the dorsal fascia (at the level of the middle part of m. *dorsalis scapulae*). The three branches insert on the articular process of the lower jaw.

*Hyla boans* (fig. 6b). It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately triangular (wider at the origin) originates on the posterior edge of the otic process of the squamosal The posterior slip, approximately triangular and wide at the origin (longer than anterior slip), originates on the dorsal fascia (at the level of the middle region of m. *dorsalis scapulae*) Both branches insert on the articular process of the lower jaw.

*Hyla andina*. It has a single *depressor mandibulae* muscle that originates from the otic process of the squamosal and the posterior edge of the *anulus tympanicus* It is approximately

Source : MNHN, Paris

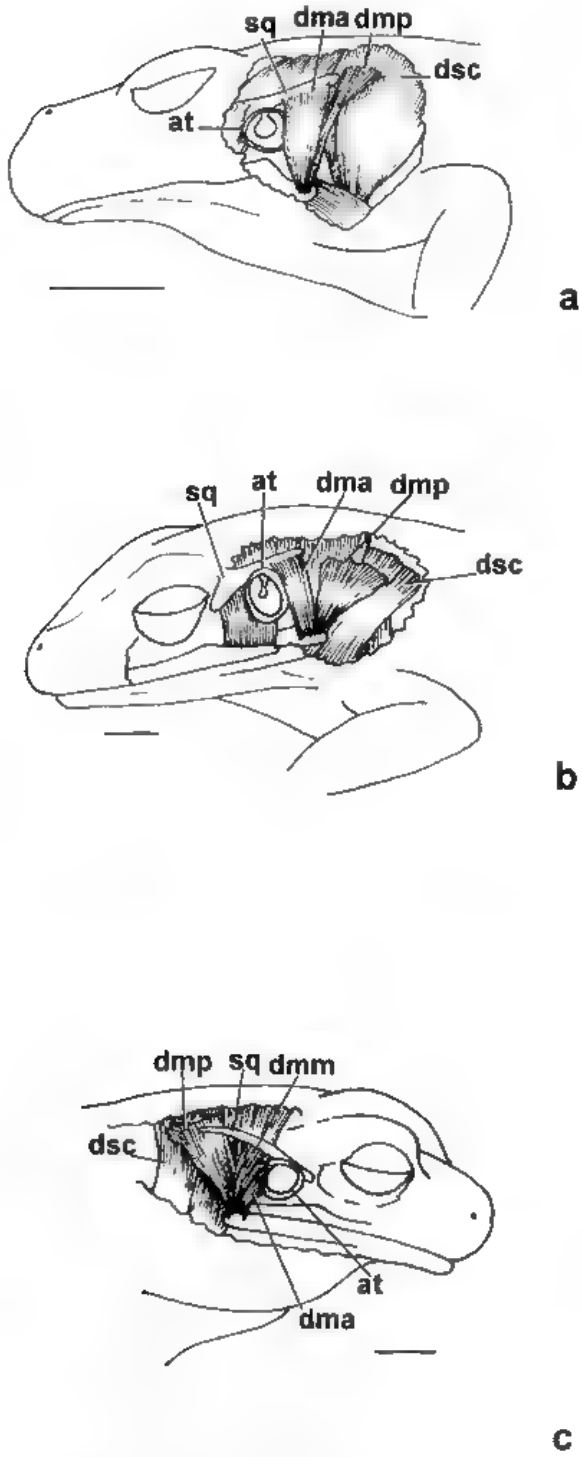



Fig. 6. — (a) *Acris crepitans* (RL 017838). Morphology corresponding to group IX (tab. 1). Scale bar 0.3 mm. — (b) *Hyla boans* (FML 09543). Morphology corresponding to group X (tab. 1). Scale bar 0.5. — (c) *Phrynohyas venulosa* (FML 02303). Morphology corresponding to group XI (tab. 1). Scale bar 0.5 mm. — Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dma, m. *depressor mandibulae anterior*; dmm, m. *depressor mandibulae medialis*; dmp, m. *depressor mandibulae posterior*; dsc, m. *dorsalis scapulae*; sq, squamosal.

Source : MNHN, Paris

triangular, wider at the origin and does not contact with m. *dorsalis scapulae* The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

*Phrynohyas venulosa* (fig. 6c) It has a *depressor mandibulae* muscle divided into three slips. The anterior slip is short and approximately rectangular and originates on the ventral edge of the *anulus tympanicus* The middle slip is wide and partially covered by the anterior slip (the otic process of the squamosal crossing over it) It originates on the epimysium of the lateral edge of m. *levator mandibulae posterioris longus*. The posterior slip, long and approximately triangular, arises from the dorsal fascia (at the level of the suprascapula) and contacts the m *levator scapulae*. The three branches insert on the articular process of the lower jaw by a thick, wide and very short tendon.

*Plectrohyla guatemalensis*. It has a *depressor mandibulae* muscle divided into two slips. The anterior slip arises from the otic process of the squamosal. It is very thin, approximately rectangular, and short. The posterior slip originates from the dorsal fascia (at the level of the mesial edge of the suprascapula). It is very wide and approximately triangular. Both branches insert on the articular process of the lower jaw.

*Ptychohyla ignicolor* It has a *depressor mandibulae* muscle divided into two slips. The anterior slip originates from the otic process of the squamosal. It is thick and approximately rectangular. The posterior slip originates from the dorsal fascia (at the level of the edge of the anterior half of the m *dorsalis scapulae*). It is very thin and approximately rectangular. Both branches insert on the articular process of the lower jaw by a short tendon

*Scinax fuscovarius* (fig 7a) It has a fan-shaped single *depressor mandibulae* muscle (wide at the origin) that originates from the dorsal fascia (at the level of the superior branch of m. *dorsalis scapulae*), otic process of the squamosal, and the anterior fibers on the posterior edge of *anulus tympanicus*. It inserts on the articular process of the lower jaw.

*Smilisca sila* It has a *depressor mandibulae* muscle divided into two slips. The anterior slip originates from the posterior end of the otic process of the squamosal. It is long, narrow, and approximately rectangular The posterior slip originates from the dorsal fascia (at the level of the mesial half of the m. *dorsalis scapulae*). It is long, thin, approximately rectangular, and curved. Both branches insert on the articular process of the lower jaw

*Phyllomedusinae*

*Agalychnis saltator* (fig 7b). It has a *depressor mandibulae* muscle divided into two slips. The anterior slip arises from the posteroventral edge of the *anulus tympanicus*. It is approximately rectangular, short, and thin The posterior slip arises from the otic process of the squamosal. It is very thick, wide, and approximately rectangular. Both branches insert on the articular process of the lower jaw

*Phyllomedusa boliviana* It has a *depressor mandibulae* muscle divided into three slips. The anterior slip originates from the posteroventral edge of the *anulus tympanicus* It is approximately rectangular, short, and thin The middle slip is approximately triangular (wider at the origin). It arises from the otic process of the squamosal, and partially covers the posterior slip, which arises from the dorsal fascia (at the level of the anterior edge of the m *dorsalis scapulae*) It is long, curved, and approximately triangular, it covers the anterior edge of the m *dorsalis scapulae* The three branches insert on the articular process of the lower jaw

Source : MNHN, Paris

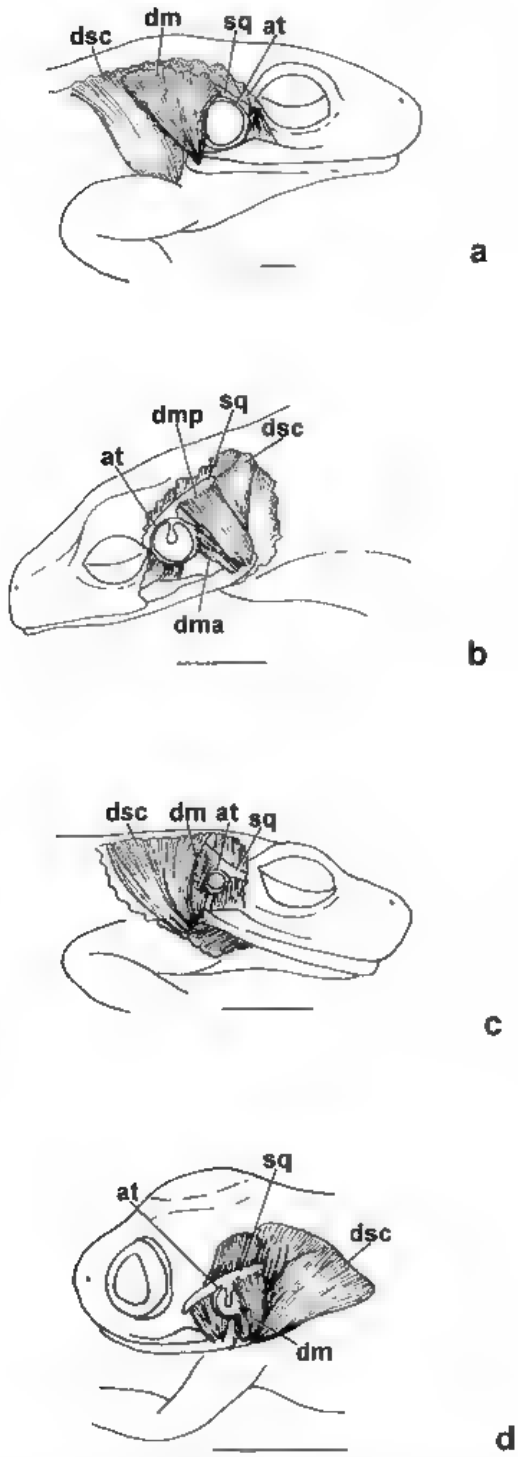



Fig. 7 (a) *Scinax fuscovarius* (FML 04635) Morphology corresponding to group IV (tab. 1) Scale bar 0 5 mm (b) *Agalychnis saltator* (FML 09541) Morphology corresponding to group VIIb (tab. 1) Scale bar 0 5 mm (c) *Centrolene grandisonae* (FML 04980) Morphology corresponding to group VIIa (tab. 1) Scale bar 0 5 mm (d) *Cochranella ignota* (UVC 12091) Morphology corresponding to group VIIa (tab. 1) Scale bar 0 5 mm Abbreviations at, *anulus tympanicus*, dm, m *depressor mandibulae*, dma, m *depressor mandibulae anterior*, dmp, m *depressor mandibulae posterior*, dsc, m *dorsalis scapulae*, sq, squamosal

Source : MNHN, Paris

*Phyllomedusa hypocondrialis*. – It has a *depressor mandibulae* muscle divided into three slips. The anterior slip originates from the ventral edge of the *anulus tympanicus* It is approximately rectangular, short, and thin The middle slip originates from the otic process of the squamosal. It is approximately rectangular, wide at the origin. The posterior slip originates from the dorsal fascia (at the level of the anterior edge of m. *dorsalis scapulae*) It is long, thin, approximately triangular, and curved. It covers the anterior edge of m. *dorsalis scapulae*. The three branches insert on the articular process of the lower jaw.

*Phyllomedusa sauvagii* It has a *depressor mandibulae* muscle divided into three slips. The anterior slip originates from the posteroventral edge of *anulus tympanicus*. It is approximately rectangular and thin. The middle slip originates from the otic process of the squamosal. It is approximately triangular (wide at the origin)and partially covers the posterior slip. The posterior slip originates from the dorsal fascia (at the level of the middle region of the m *dorsalis scapulae*) It is long and approximately rectangular. It covers the anterior half of the m. *dorsalis scapulae* The three branches insert on the articular process of the lower jaw

FAMILY CENTROLENIDAE

*Centrolene grandisonae* (fig 7c). It has a single *depressor mandibulae* muscle. It originates on the posterior edge of the *anulus tympanicus* and the otic process of the squamosal It is short, small and approximately triangular It does not contact the m. *dorsalis scapulae* The m. *depressor mandibulae* inserts on the articular process of the lower jaw.

*Cochranella ignota* (fig. 7d). It has a *depressor mandibulae* muscle divided into two slips. The anterior slip arises from the posteroventral edge of the *anulus tympanicus*. It is approximately rectangular, short, and thin The posterior slip is approximately triangular and it originates on the otic process of the squamosal. It does not contact the m. *dorsalis scapulae*. It inserts on the articular process of the lower jaw.

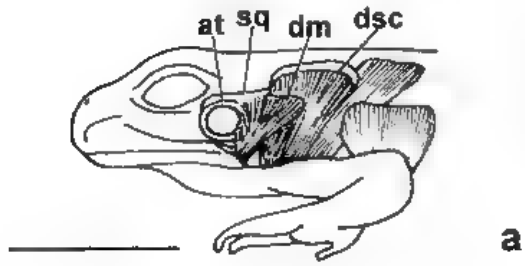
FAMILY PSEUDIDAE

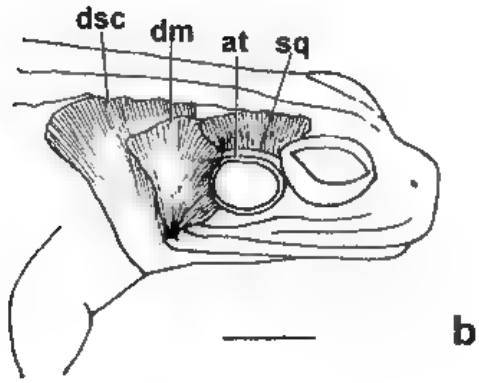
*Lysapsus limellus* (fig. 8a) It has a single *depressor mandibulae* muscle. It originates on the posterior edge of the *anulus tympanicus*, the otic process of the squamosal, and the dorsal fascia. The m. *depressor mandibulae* is approximately triangular, wider at the origin, and contacts the m *dorsalis scapulae* The m *depressor mandibulae* inserts on the articular process of the lower jaw.

*Pseudis minutus* (fig 8b) It has a single *depressor mandibulae* muscle that originates on the posterior edge of the *anulus tympanicus*, the otic process of the squamosal, and the dorsal fascia It is a very thick, wide and fan-shaped muscle that contacts the m. *dorsalis scapulae* The m *depressor mandibulae* inserts on the articular process of the lower jaw

*Pseudis paradoxus* (fig 8c). – It has a single *depressor mandibulae* muscle. It originates on the posterior edge of the *anulus tympanicus*, the otic process of the squamosal, and the dorsal fascia. It is a long, fan-shaped muscle, which contacts the m. *dorsalis scapulae*. The m. *depressor mandibulae* inserts on the articular process of the lower jaw

Source : MNHN, Paris



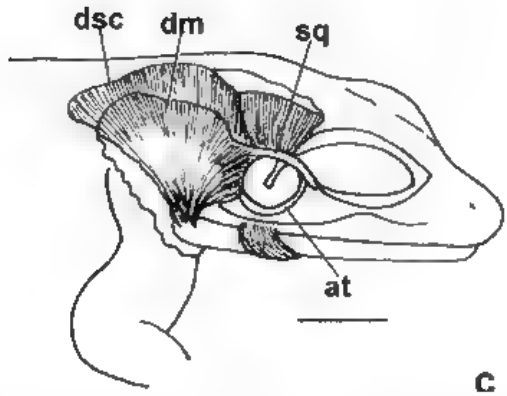




Fig. 8 (a) *Lysapsus limellus* (FML 00791) Morphology corresponding to group IV (tab. 1) Scale bar 0.5 mm (b) *Pseudis minutus* (FML 03676) Morphology corresponding to group IV (tab. 1) Scale bar 0.5 mm (c) *Pseudis paradoxus* (FML 00936) Morphology corresponding to group IV (tab. 1) Scale bar 0.5 mm Abbreviations: at, *anulus tympanicus*, dm, m. *depressor mandibulae*, dsc, m. *dorsalis scapulae*; sq, squamosal

Source : MNHN, Paris

FAMILY MICROHYLIDAE

*Brevicipitinae*

*Breviceps poweri* (fig 9a). It has a *depressor mandibulae* muscle divided into two slips. The anterior slip originates on the posterior end of the maxilla by a short tendon. It is thick, short, and approximately fusiform. The posterior slip originates on the otic process of the squamosal This slip is long, thick, and approximately triangular Both branches insert on the articular process of the lower jaw.

*Microhylinae*

*Dermatonotus muelleri* (fig 9b). It has a *depressor mandibulae* muscle divided into two slips. The anterior slip originates on the ventral edge of the *anulus tympanicus* It is short, thick, and approximately rectangular The posterior slip originates from the dorsal fascia (at the level of the mesial edge of the m. *dorsalis scapulae* and the m. *latissimus dorsi*, almost reaching the posterior edge of the eyes). It is long, thick, approximately triangular, and very wide at the origin. Both branches insert on the articular process of the lower jaw.

*Elachistocleis bicolor* (fig. 9c). – It has a single *depressor mandibulae* muscle It originates from the ventral and anterior edge of the *anulus tympanicus* and the dorsal fascia (at the level of the anterior edge of the m. *dorsalis scapulae* and the m. *latissimus dorsi*). The m *depressor mandibulae* is a very wide and fan-shaped muscle that partially covers the tympanum, the jugal and the posterior edge of the maxilla. A branch of cranial nerve VII passes through it. The muscle inserts on the articular process of the lower jaw

*Phrynomerinae*

*Phrynomantis bifasciatus*. It has a *depressor mandibulae* muscle divided into two slips. The anterior slip originates on the lateral edge of the *anulus tympanicus*. It is short, thick, and approximately rectangular The posterior slip originates on the dorsal fascia, and covers the mesial edge of the m *cucullaris* and the anteromedial edge of the m *dorsalis scapulae* It is a fan-shaped muscle with a longer posterodorsal projection It surrounds the posterior edge of the tympanum A branch of cranial nerve VII passes through it. Both branches insert on the articular process of the lower jaw.

FAMILY DENDROBATIDAE

*Colostethus subpunctatus* It has a *depressor mandibulae* muscle divided into two slips. The superficial slip originates from the dorsal fascia (at the level of the m. *dorsalis scapulae* and the m. *levator mandibulae posterioris longus*). It is a wide and fan-shaped muscle The deep slip originates on the posterior edge of the *anulus tympanicus* and the otic process of the squamosal It is short, small, and rectangular Both branches insert on the articular process of the lower jaw.

*Dendrobates auratus* (fig. 10a). It has a *depressor mandibulae* muscle partially divided into three slips. The anterior slip originates from the dorsal fascia (at the level of the m *dorsalis scapulae* and the m. *levator mandibulae posterioris longus*). It is approximately triangular and

Source : MNHN, Paris

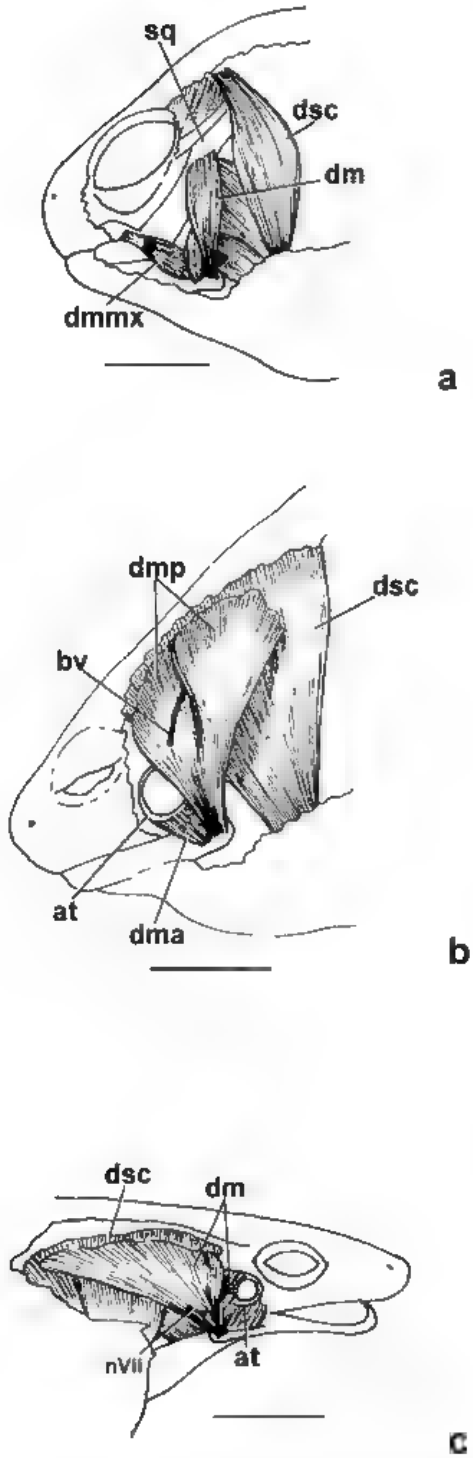



Fig. 9. (a) *Breviceps poweri* (FML 03165). Morphology corresponding to group VIc (tab. 1). Scale bar: 0.5 mm. (b) *Dermatonotus muelleri* (FML 05365). Morphology corresponding to group XIIb (tab. 1). Scale bar: 0.5 mm. (c) *Elachistocleis bicolor* (FML 00251). Morphology corresponding to group XIIa (tab. 1). Scale bar: 0.5 mm. Abbreviations: at, *anulus tympanicus*; dm, m. *depressor mandibulae*; dma, m. *depressor mandibulae anterior*; dmmx, m. *depressor mandibulae maxilaris*; dmp, m. *depressor mandibulae posterior*; dsc, m. *dorsalis scapulae*; bv, branch of the nerve VII; sq, squamosal.

Source : MNHN, Paris

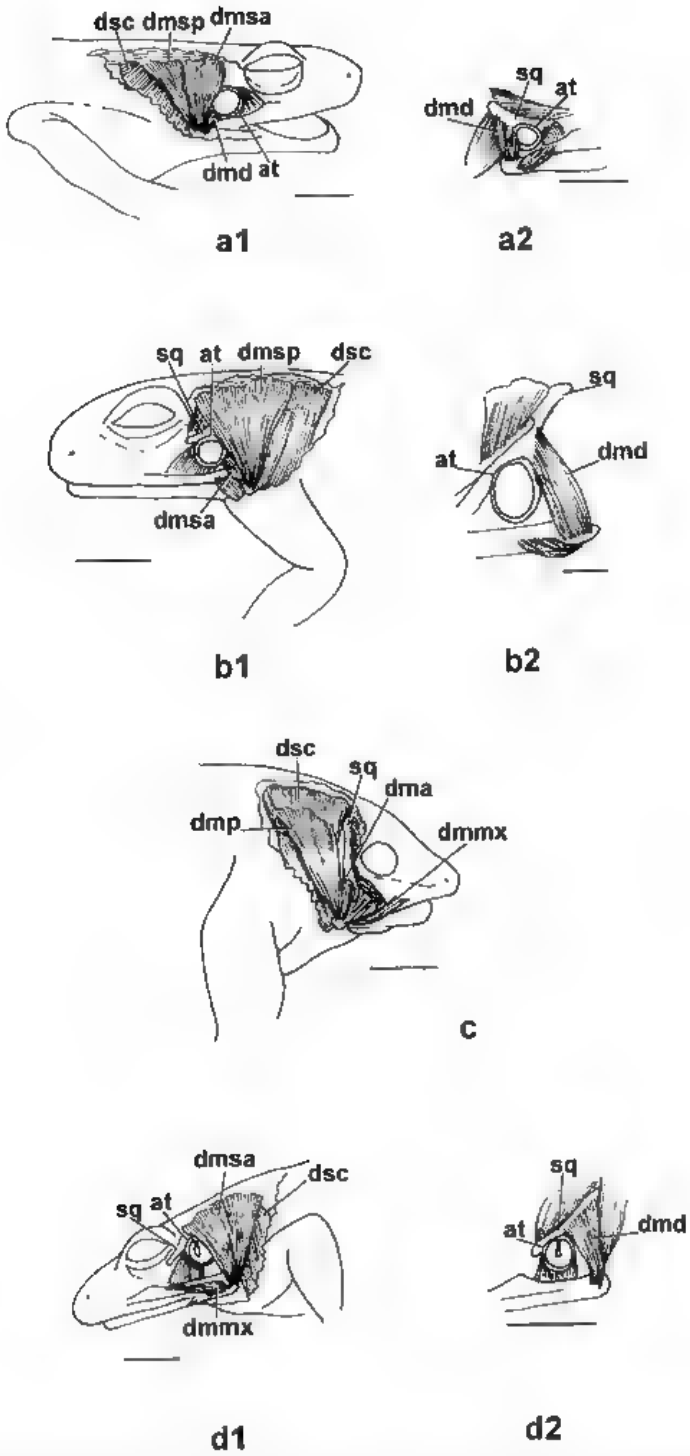



Fig. 10 (a1) *Dendrobates auratus* (FML 01722) Morphology corresponding to group Vb (tab. 1). Scale bar 0 5 mm (a2) Detail of deep m *depressor mandibulae* of *D. auratus*. Scale bar 0 5 mm – (b1) *Epipedobates pictus* (FML 03516). Morphology corresponding to group Vd (tab. 1) Scale bar. 0 3 mm (b2) Detail of deep m. *depressor mandibulae* of *E. pictus*. Scale bar. 0 1 mm – (c) *Hemisus guineensis guineensis* (FML 01244) Morphology corresponding to group VIa (tab. 1) Scale bar 0.5 mm (d1) *Arthroleptis tuberosus* (FML 00051) Morphology corresponding to group VIb (tab. 1) Scale bar 0 3 mm (d2) Detail of deep m *depressor mandibulae* of *A. tuberosus* Scale bar 0 3 mm Abbreviations at, *anulus tympanicus*, dma, m *depressor mandibulae anterior*, dmd, deep m *depressor mandibulae*, dmmx, m. *depressor mandibule maxilaris*, dmp, m *depressor mandibulae posterior*, dmsa, m *depressor mandibulae superficial anterior*, dmsp, m *depressor mandibulae superficial posterior*; dsc, m. *dorsalis scapulae*; sq, squamosal

Source : MNHN, Paris

wider at the origin. The posterior slip originates from the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is approximately rectangular and as long as the anterior slip. A deep slip originates on the posterior edge of the *anulus tympanicus* and the otic process of the squamosal. It is short, approximately rectangular, wide at the origin. The three branches insert on the articular process of the lower jaw.

*Epipedobates pictus* (fig. 10b) – It has a *depressor mandibulae* muscle divided into two slips; the superficial one is partially divided. The anterior superficial slip, which is short and rectangular, originates on the posterior edge of the *anulus tympanicus*. The posterior superficial slip originates from the dorsal fascia (at the level of the posterolateral region of the anteromesial part of the m. *dorsalis scapulae*). A deep slip, narrow and rectangular, originates on the otic process of the squamosal and the posteroventral edge of the *anulus tympanicus*. The three branches insert on the articular process of the lower jaw, the deep slip mesial to superficial slips.

## Family Hemisotidae

*Hemisus guineensis guineensis* (fig. 10c) – It has a *depressor mandibulae* muscle divided into three slips. The anterior slip, short and fusiform, originates on the alary process of the maxilla by a tendon. The middle rectangular slip originates on the otic process of the squamosal. The posterior slip originates on the dorsal fascia (at the level of the suprascapula, partially covering the m. *dorsalis scapulae* and the m. *latissimus dorsi*). It is triangular and broad, curving toward the posterior region of the body. The three branches insert on the posterior end of the quadrate.

## Family Arthroleptidae

### *Arthroleptinae*

*Arthroleptis tuberosus* (fig. 10d) – It has a *depressor mandibulae* muscle divided into three slips. The anterior superficial slip originates on the posterior edge of the maxilla. It is long, very thin, and approximately fusiform. The posterior superficial slip is fan-shaped and wide at its origin on the dorsal fascia. It partially covers the m. *dorsalis scapulae* and m. *latissimus dorsi*, and completely covers the deep slip. The deep slip, approximately rectangular and slightly wider at its origin, originates on the otic process of the squamosal. It partially covers the posterior border of the tympanum. The three branches insert on the articular process of the lower jaw.

*Arthroleptis stenodactylus stenodactylus* – It has a *depressor mandibulae* muscle divided into three slips. The anterior superficial slip originates on the posterior edge of the maxilla. It is long, very thin, and approximately fusiform. The posterior superficial slip, fan-shaped and wide at its origin on the dorsal fascia, covers the m. *dorsalis scapulae* and m. *latissimus dorsi*. The deep slip, approximately rectangular, originates on the otic process of the squamosal. It partially covers the posterior border of the tympanum. The three branches insert on the articular process of the lower jaw.

Source : MNHN, Paris

*Schoutedenella* sp. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and rectangular, is wide at the origin and originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip, fan-shaped and wider at the origin, originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). Its posterior part partially covers the suprascapula. Both branches insert on the articular process of the lower jaw.

*Schoutedenella sylvatica*. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and rectangular, is wide at the origin and originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is fan-shaped and wider at the origin with a posterior part that partially covers the suprascapula. Both branches insert on the articular process of the lower jaw.

*Cardioglossa* sp. (fig. 11a). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip is short, rectangular, and thick, originating from the otic branch of the squamosal at the posteroventral edge of the *anulus tympanicus*. The posterior slip is fan-shaped and wider at the origin, originating on the dorsal fascia (at the level of the m. *dorsalis scapulae* and the m. *rhomboideus* anterior). A nerve V branch passes through its fibers at mid-level. This slip partially covers the anterior slip. Both branches insert on the articular process of the lower jaw.

## FAMILY RANIDAE

### *Dicroglossinae*

*Conraua crassipes*. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and approximately rectangular, originates on the inferior edge of the *anulus tympanicus*. The posterior fan-shaped slip, wider at the origin, originates on the dorsal fascia (at the level of the dorsal part of the m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw by a short tendon.

*Hoplobatrachus occipitalis*. – It has a single *depressor mandibulae* muscle. It originates on the inferior edge of the *anulus tympanicus* and the dorsal fascia (at the level of the anterodorsal part of the m. *dorsalis scapulae*, covering most of it). The *depressor mandibulae* is a fan-shaped and very wide muscle. It inserts on the articular process of the lower jaw by a short tendon.

### *Ptychadeninae*

*Ptychadena mascareniensis hylaea*. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and approximately rectangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip, thin and approximately triangular, is wider at the origin and originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

### *Pyxicephalinae*

*Aubria subsigillata* (fig. 11b). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short, thick, and approximately rectangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior fan-shaped slip is flat and wider at the origin, and

Source : MNHN, Paris

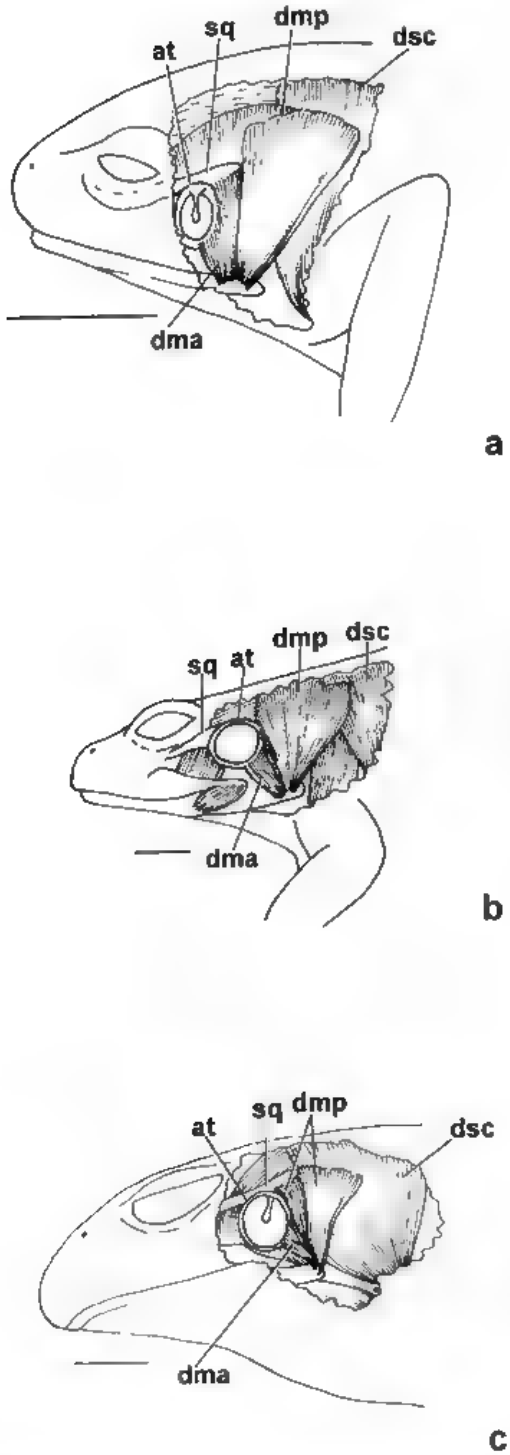



Fig. 11. (a) *Cardioglossa cyaneospila* (FML 06477). Morphology corresponding to group XV (tab. 1). Scale bar: 0.5 mm. (b) *Aubria subsigillata* (FML 03154). Morphology corresponding to group XIIb (tab. 1). Scale bar: 0.5 mm. (c) *Rana angolensis* (FML 03188). Morphology corresponding to group Va (tab. 1). Scale bar: 0.5 mm. Abbreviations: at, *anulus tympanicus*, dma, m. *depressor mandibulae anterior*, dmp, m. *depressor mandibulae posterior*, dsc, m. *dorsalis scapulae*, sq, squamosal.

Source : MNHN, Paris

originates on the dorsal fascia. It partially covers the m. *dorsalis scapulae* and m. *latissimus dorsi*. Both branches insert on the articular process of the lower jaw.

*Raninae*

*Rana albolabris*. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and approximately triangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia covering the m. *dorsalis scapulae*. Both branches insert on the articular process of the lower jaw.

*Rana angolensis* (fig. 11c). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and approximately rectangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is a fan-shaped slip, wider at the origin and partially covers the anterior slip. Both branches insert on the articular process of the lower jaw.

*Rana lepus*. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip originates on the inferior edge of the *anulus tympanicus*. It is short thick and approximately rectangular. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*) and is fan-shaped and wider at the origin, with the fibers partially divided. Both branches insert on the articular process of the lower jaw.

## FAMILY PETROPEDETIDAE

*Phrynobatrachus acutirostris* (fig. 12a). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and approximately rectangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is approximately triangular, flat, thin and wider at the origin. Both branches insert on the articular process of the lower jaw.

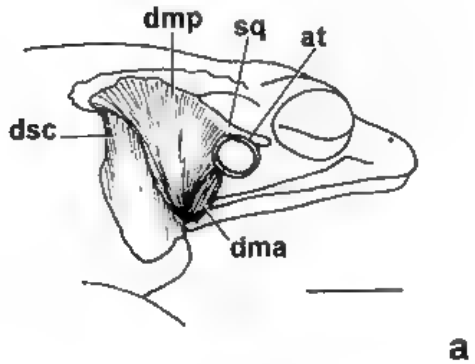
*Phrynobatrachus calcaratus*. – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short and approximately rectangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is approximately triangular, flat, thin and wider at the origin. A nerve V branch passes through its fibers at mid-level. Both branches insert on the articular process of the lower jaw.

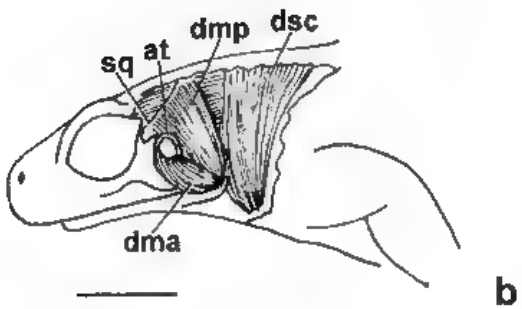
## FAMILY HYPEROLIIDAE

*Hyperoliinae*

*Afrixalus orophilus* (fig. 12b). – It has a *depressor mandibulae* muscle divided into two branches. The anterior slip, approximately rectangular and narrow, originates on the anteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *levator mandibulae posterioris longus*), and the posterior edge of the *anulus tympanicus*. It is approximately triangular and wider at the origin. Both slips partially surround the tympanum. Both branches insert on the articular process of the lower jaw by a short and thin tendon.

Source : MNHN, Paris



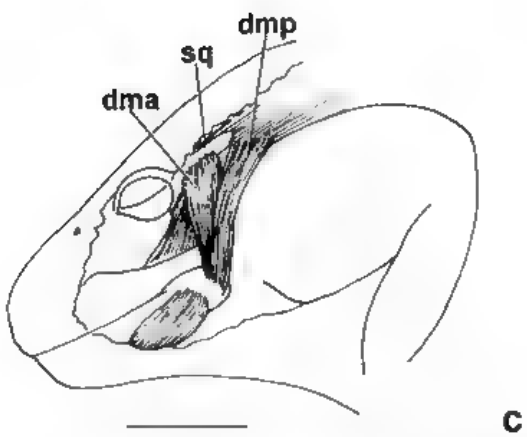




Fig 12 (a) *Phrynobatrachus acutirostris* (DIAM 006) Morphology corresponding to group Va (tab. 1) Scale bar 0 5 mm (b) *Afrixalus orophilus* (FML 03229) Morphology corresponding to group XIV (tab. 1). Scale bar 0 3 mm (c) *Rhinophrynus dorsalis* (FML 01720). Morphology corresponding to group IX (tab. 1) Scale bar 0.5 mm. – Abbreviations: at, *anulus tympanicus*; dma, m. *depressor mandibulae anterior*, dmp, m *depressor mandibulae posterior*; dsc, m. *dorsalis scapulae*, sq, squamosal

Source : MNHN, Paris

*Chrysobatrachus cupreonitens.* – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately rectangular, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is fan-shaped, wider and very thin at the origin, and thicker and narrower at the insertion point. The posterior slip partially covers the anterior slip. Both branches insert on the articular process of the lower jaw.

*Kassininae*

*Kassina senegalensis angeli.* – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately rectangular and short, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is triangular, wider at the origin with a nerve V branch passing through it. This slip partially covers the anterior slip. Both branches insert on the articular process of the lower jaw by a short tendon.

*Leptopelinae*

*Leptopelis notatus.* – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, short, bulky and approximately fusiform, originates on the posteroventral edge of the *anulus tympanicus*. The posterior slip originates on the dorsal fascia (at the level of the m. *dorsalis scapulae*). It is triangular, very wide at the origin and partially covers the anterior slip. Both branches insert on the articular process of the lower jaw.

FAMILY RHINOPHRYNIDAE

*Rhinophrynus dorsalis* (fig. 12c). – It has a *depressor mandibulae* muscle divided into two slips. The anterior slip, approximately triangular and elongated, originates on the otic process of the squamosal. The posterior slip, very narrow, thin, and curved, originates on the dorsal fascia (at the level of the middle part of m. *dorsalis scapulae*). Both branches insert on the articular process of the lower jaw.

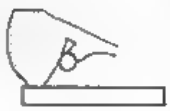
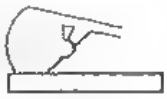
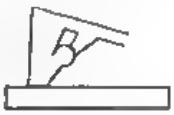
## DISCUSSION

There is a considerable variation in the morphology of the m. *depressor mandibulae*. Nevertheless, fifteen morphological groups can be distinguished within the anuran species analysed (tab. 1). Although many studies have shown that the variation of the jaw muscles involves either their origin or insertion (ECKER, 1889, BEDDARD, 1908, 1911, EDGEWORTH, 1935, BALDAUF, 1955), in these fifteen groups, the insertion points of the m. *depressor mandibulae* is relatively invariant (see BAUER, 1997). The area of the origin on the posterior region of the head is also stable (allowing the muscle to open the mouth), except in *Hemisus*, *Arthroleptis* and *Breviceps* which have an extra anterior branch coming from the maxilla. Most variation involves muscle shape and often demonstrates intra- or intergeneric variation.

We found the following variation in the taxa analysed.

Source : MNHN, Paris

Table 1. Schematic representation of the different conditions of the *depressor mandibulae* muscle in anurans, with notation following STARRETT (1968) and modifications in this work. Each group is identified by a Roman number (I to XV). Different morphotypes in a same group are identified by a letter (a, b, c or d). Superficial and deep slips of the *depressor mandibulae* muscle, when present, are identified by a subindex (1 and 2, respectively)

| Group | Scheme | | Taxa | STARRETT, 1968 | Present work |
|---|---|---|---|---|---|
| I | | | *Xenopus*<br>*Alytes* | Dfsq<br>DFa | Dfa<br>DFa |
| II |  | a | *Chacophrys* | DFSQAT | DFSQ |
| | | b | *Bufo arenarum*; *B. paracnemis*;<br>*B. spinulosus*<br>*Rhinophrynus*; *Melanophryniscus* | ——<br>SQ | SQ<br>SQ |
| |  | c | *B. g. major*; *Lepidobatrachus*; *Crinia*<br>*Ceratophrys*<br>*Hymenochirus* | ——<br>DFSQAT<br>SQ | Sqat<br>SQat<br>SQat |
| III | | | *Leptodactylus bufonius*; *L. chaquensis*,<br>*Physalaemus biligonigerus*;<br>*Crossodactylus*; *Taudactylus* | —— | DFsq |
| IV | | | Pseudidae; *Scinax*<br>*Gastrotheca*<br>*Hyla andina* | ——<br>*DFsq*<br>DF | Dfsqat<br>*DFsqat*<br>Dfsqat |
| V | | a1 | | | |
| | | a2 | *Limnodynastes fletcheri*; *L. dorsalis*;<br>*L. ornatus*; *Phrynobatrachus*;<br>*Rana angolensis*; *Uperoleia borealis* | —— | DFSQ-at$_d$ |
| | | b1 | | | |
| |  | b2 | *Dendrobates* | DFSQ$_d$at | DF-DF-sqat$_d$ |

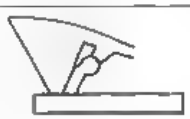
Source : MNHN, Paris

Table 1. – (Continuation)

| Group | Scheme | | Taxa | STARRETT, 1968 | Present work |
|---|---|---|---|---|---|
| V (cont.) | | c1 | | | |
| | | c2 | *Colostethus*; *Limnodynastes dumerili*<br>*Pseudopaludicola boliviana* | -----<br>DFSQ$_d$AT | DF-sqat$_d$<br>DF-sqat$_d$ |
| | | d1 | | | |
| | | d2 | *Epipedobates* | ----- | DF-at-sq$_d$ |
| VI | | a | *Hemisus g. guineensis* | ----- | DF-sq-mx |
| | | b1 | | | |
| | | b2 | *Arthroleptis tuberosus*; *A. s. stenodactylus* | ----- | DF-sq$_d$-mx |
| | | c | *Breviceps* | ----- | sq-mx |
| VII | | a | Centrolenidae<br>*Rhinoderma* | Dfa<br>SQ | Sqat<br>Sqat |
| | | b | *Agalychnis* | ----- | SQ-at |
| VIII | | | *Phyllomedusa*<br>*Argenteohyla* | SQ<br>----- | DF-SQ-at<br>DF-SQ-at |
| IX | | | *Acris*, *Notaden*; *Ptychohyla*; *Smilisca*<br>*Rhinophrynus* | -----<br>SQ | df-SQ<br>df-SQ |

Source : MNHN, Paris

Table I. – (Continuation)

| Group | Scheme | | Taxa | STARRETT, 1968 | Present work |
|---|---|---|---|---|---|
| X | | | *Hyla boans*; *Pleurodema borelli*, | ----- | DF-sq |
| | | | Telmatobiinae | | |
| | | | *Plectrohyla* | DF | DF-sq |
| XI | | | *Phrynohyas* | ----- | DF-DF-at |
| XII | | a | *Elachistocleis*, *Hoplobatrachus* | ----- | DFat |
| | | | *Aubria*; *Chrysobatrachus*; *Conraua*; *Dermatonotus*; *Leptopelis*; *Phrynobatrachus*; *Phrynomantis*; *Ptychadena*; *Rana alboiabris*; *R. lepus*; *Schoutedenella* | ----- | DF-at1 |
| | | b | *Kassina* | DF AT | DF-at1 |
| | | c | *Limnodynastes convextusculus* | ----- | DF-at2 |
| XIII |  | | *Uperoleia aspera* | ----- | DFSQat |
| XIV | | | *Afrixalus orophilus* | ----- | DFsq-at |
| XV | | | *Cardioglossa* | ----- | DF-sqat |

Pipids and discoglossids have a single m. *depressor mandibulae*. STARRETT (1968) found that the apparent single muscle in *Xenopus* is a tripartite muscle, not very differentiated, but with three different origins (*anulus tympanicus*, dorsal fascia and squamosal). The only origin of the muscle on the dorsal fascia in our observations, with no apparent divisions, lead us to consider the m. *depressor mandibulae* morphology in *Xenopus* as a single one. Our descriptions of the *Alytes* m. *depressor mandibulae* agree with STARRETT's. However, in her descriptions, *Alytes* and *Xenopus* have different morphological patterns. In our case both taxa belong to the same group I.

Source : MNHN, Paris

Interestingly, both of these groups traditionally considered basal related to the Neobatrachia (FORD & CANNATELLA, 1993, CANNATELLA, 1999, MAGLIA et al., 2001; HAAS, 2001) have a simple morphology of the m. *depressor mandibulae*, with an origin on the dorsal fascia GRIFFITHS (1954) considered this state the primitive morphology of the muscle; but STARRETT (1968) did not agree with his hypothesis. *Hymenochirus* has a bulky m. *depressor mandibulae* like bufonids. This morphology was observed by STARRETT (1968) in some isolated species of different families. This situation is described by her also in *Rhinophrynus*. We could not find any fibers arising from the crista parotica in *Rhinophrynus dorsalis* as STARRETT (1968) described; we observed that all the muscle origins are at the otic ramus of the squamosal.

The Bufonidae analysed have a single bulky muscle similar to *Lepidobatrachus llanensis*, *Ceratophrys cranwelli* and *Chacophrys pierotti* (Leptodactylidae, Ceratophryinae) (group II, tab. 1). Ceratophryines have been considered alternatively related to bufonids (LIMESES, 1965), as a subfamily of the Leptodactylidae (Ceratophryinae) (LYNCH, 1973; HEYER, 1975; DUELLMAN & TRUEB, 1985) or a separate family (REIG, 1972). The particular morphology of the *depressor mandibulae* muscle in the Bufonidae (also considered by STARRETT, 1968, as a single slip with a non-fascial origin), seems to be a conservative condition and could be considered a primary homology shared by the Ceratophryinae-Bufonidae groups.

We found three more morphological patterns (groups III, V and X) for the rest of leptodactylids analysed. Only the species included in our group III have the pattern considered by STARRETT (1968) as the common type of the family, which includes origin from the squamosal. However, the inclusion of *Crossodactylus* in this group is at odds with her results. PALAVECINO (2000), analysing four of our species (*Physalaemus biligonigerus*, *Leptodactylus chaquensis*, *L. bufonius* and *Pleurodema borellii*), found very different patterns. All the species, except *P borellii*, are in our group III. The most striking difference is that in her results the m. *depressor mandibulae* origin never includes the squamosal (as it is in STARRETT, 1968, and in our results) This difference is probably related with the age (stage) of the specimens analysed. Another difference involves the *anulus tympanicus* that in our results in no case has any m *depressor mandibulae* fiber attached.

HEYER (1975) found six character states of the m. *depressor mandibulae* morphology in the leptodactylid frogs he analysed Among the genera analysed here, ten were also observed by him. Some of his results are coincident with ours. *Crossodactylus*, *Leptodactylus* and *Physalaemus* share the same pattern, described as B by HEYER (1975), and are together in our group III. In the other cases there are no coincidences at all.

Among hylids, we found seven different m *depressor mandibulae* morphologies (tab. 1) Within the genus *Phyllomedusa* we considered only those species with grasping feet All these species have the same morphological type of the *depressor mandibulae* muscle with three branches ("*partes*: *pars tympanica*, *pars squamosal* and *pars scapularis*") (group VIII, tab 1), similar to *Phyllomedusa atelopoides* (MANZANO, 1997), *P perinesos* (DUELLMAN, 1973), *P tomopterna* and *P tarsius* (CANNATELLA, 1980) The *Phyllomedusa buckleyi* group lacks the posterior branch of the *depressor mandibulae* muscle ("*pars scapularis*") as does *Agalychnis* (CANNATELLA, 1980) This particular condition was previously mentioned as one of the synapomorphies of the *buckleyi* group, suggesting that the genus *Phyllomedusa* is an unnatural assemblage of species (CANNATELLA, 1980) Moreover, some authors considered that the *buckleyi* group should be accorded generic status (DUELLMAN, 1968, 1969), representing a

Source : MNHN, Paris

separate group closer to *Agalychnis* than to *Phyllomedusa*. All the species of this genus analysed by STARRETT (1968), including *P. boliviana*, have the condition SQ. We found that *P. boliviana* and the other two species of this genus have the condition DF-SQ-at. The morphology of the m. *depressor mandibulae* in *Agalychnis saltator* (group VIIb) is similar to that of centrolenids described here (group VIIa), a condition also observed by RUEDA-ALMONCAID (1994) in *Centrolene geckoideum*. However, there is a big variation within the Centrolenidae, exhibiting a *depressor mandibulae* muscle composed of two or three branches and different designs (MANZANO, 2000), so the character is of limited usefulness in the comparison of both groups. STARRETT (1968) considered a single slip lying over the squamosal as the pattern of adult centrolenids, but her results disagree with MANZANO (2000) and ours.

Within the Hylinae, a large morphological diversity makes it impossible to assign them a single defined pattern. For example, *Acris crepitans*, *Ptychohyla ignicolor* and *Smilisca sila* have a morphotype similar to that of *Notaden* (a Myobatrachidae) and *Rhinophrynus dorsalis* (a Rhinophrynidae) (group IX, tab. 1). Our results disagree with STARRETT's (1968). She found that *Acris* and *Ptycholyla* have a DF condition instead of df-SQ as in our specimens. In her results *Smilisca* has the condition DFsq, instead of df-SQ as in ours. *Hyla andina* and *Scinax fuscovarius* have a morphotype similar to that found in the Pseudidae and *Gastrotheca* (a Hemiphractinae hylid) (group IV, tab. 1). In our results, *Gastrotheca* has the condition DFsqat. STARRETT (1968) found that the only hylid presenting an origin including the *anulus tympanicus* is *Cryptobatrachus fuhrmanni*. The morphology of the *depressor mandibulae* muscle in *Hyla boans* and *Plectrohyla guatemalensis* is similar to the Telmatobinae (Leptodactylidae) analysed and *Pleurodema borellii* (another leptodactylid) (group X, tab. 1). *Argenteohyla siemersii* has a morphology similar to that of the *Phyllomedusa* species analysed (group VIII). *Phrynohyas venulosa* has a morphology that differs from other groups and also from the rest of the hylids (group XI). Adding to this, STARRETT (1968) found individual variation for the m. *depressor mandibulae* morphology in a series of *Hyla crucifer* from the same locality. No intraspecific variation was found in *Hyla* in this study.

The pseudids analysed (group IV, tab. 1) have a very characteristic morphological pattern of the m. *depressor mandibulae*, that is also present in *Scinax fuscovarius*, *Gastrotheca* and *Hyla andina*. This group includes species with the condition DFsqat. STARRETT (1968) found the condition DFa for *Pseudis paradoxa*, again at odds with our results. It is interesting that DA SILVA (1999) hypothesized in his phylogenetic analysis a relationship between Pseudidae and Hylinae.

Another example of intrageneric variation is found in the family Myobatrachidae. Within this family, *Limnodynastes fletcheri*, *L. dorsalis* and *L. ornatus* (Limnodynastinae) and *Uperoleia borealis* (Myobatrachinae) have similar morphologies (group Va, tab. 1) that differ from the rest of the myobatrachids previously analysed (*Limnodynastes convexiusculus*, group XIIc, *Crinia georgiana*, group IIc, and *Taudactylus diurnus*, group III). *Uperoleia aspera*, group XIV (Myobatrachinae) also presents a distinctive morphotype, not shared by other myobatrachids (groups Va and Vc, tab. 1). *Notaden* (Limnodynastinae) (group IX) does not share the myobatrachid morphology of the *depressor mandibulae* muscle.

STARRETT (1968) described a *depressor mandibulae* muscle represented by three branches for the Dendrobatidae: two superficial, originating on the dorsal fascia and the *anulus tympanicus*, and a deep branch originating on the squamosal (based on *Epipedobates pictus*).

Source : MNHN, Paris

The condition that we observed in *Colosthetus subpunctatus* (group Vc, tab. 1) was also described by MYERS et al. (1991) for *Aromobates* and by LA MARCA (1995) for *Mannophryne*. In this case, the m. *depressor mandibulae* has two branches. Thus, there are at least two character states for the family with variation in the superficial branch. The particular disposition of the branches in relation to associated skull elements is common to most dendrobatids, which is why we insist on the existence of a characteristic morphotype for the family (groups Vb, Vc and Vd, tab. 1). In fact, MYERS & FORD (1986), FORD (1989) and FORD & CANNATELLA (1993) considered the arrangement of the superficial slip of the m. *depressor mandibulae* as a synapomorphy of the Dendrobatidae.

The condition of the *depressor mandibulae* muscle in *Dermatonotus* and *Elachistocleis*, group XII (Microhylinae) is similar to that described by BURTON (1983*b*) for other microhylids. Three origin points of the muscle are present in all microhylids analysed by him, except for the *Albericus* and *Choerophryne* data of Burton. *Breviceps poweri* (group VIc) has a morphology of the m. *depressor mandibulae* shared by *Arthroleptis* (group VIb) and *Hemisus* (group VIa). The morphotype of Microhylinae and Phrynomerinae *depressor mandibulae* is shared by some Ranidae (group XIIb), also mentioned by HOYOS (1999), including a nerve V branch that runs through the superficial slip of the muscle in most of the microhylids. This branch is also present in a leptodactylid, *Pseudopaludicola boliviana* (group Vc) and in an arthroleptid, *Cardioglossa* (group XV). STARRETT (1968) considered the pattern for the species of ranids as DFAT and DFSQAT. We define also two morphotypes: DFat and DF-at, but neither of them includes a squamosal origin. HOYOS (1999) found a third branch arising from the squamosal. Although we could not find this branch, we agree with him with respect to sampling matters since we did not analyse all the same species.

The variation in our analysis far exceeds that described by STARRETT (1968). In fact, we found only weak coincidences among her and our patterns (bufonids and some leptodactylids).

This leads us to believe that despite the great number of specimens analysed by various authors (GAUPP, 1896, BIGALKE, 1926; REIG & LIMESES, 1963; LIMESES, 1965, 1969; STARRETT, 1968; MCDIARMID, 1971, HEYER, 1975; EMERSON, 1976, CANNATELLA, 1980; TYLER & DAVIES, 1980; DAVIES & BURTON, 1982; BURTON, 1983*a b*; LYNCH, 1986, 1993, CANNATELLA & TRUEB, 1988; MYERS et al., 1991, WAKE, 1993, RUEDA-ALMONACID, 1994, BURTON & ZWEIFEL, 1995, LA MARCA, 1995, MANZANO, 1997, 2000, HOYOS, 1999), examination of additional specimens will doubtless uncover additional variation. Our frequent disagreement with STARRETT (1968), HEYER (1975), HOYOS (1999) or PAVLICINO (2000) constitutes the rule rather than the exception. We think that this situation expresses the true characteristic of this muscle: its extreme variability. We agree with LYNCH's (1973) conclusion that this muscle is of little use to analyse the relationships of eleutherodactyline frogs, and further extend his conclusion to the majority of the taxa observed by us.

The great diversity of the m. *depressor mandibulae* correlates with the plethora of patterns mentioned by TRUEB (1993) for cranial morphology in Anura.

We find no evidence that variations in the m. *depressor mandibulae* are associated with particular habits. For example, *Hemisus g. guineensis* (group VIa, tab. 1) has a distinct morphology of the *depressor mandibulae*, formed by three well-differentiated slips with a particular anterior branch originating on the alary process of the maxilla by a tendon. This

Source : MNHN, Paris

morphology can be interpreted as a muscle modification in relation to the animal's excavating habits, and the variation in the origin of this branch can be explained according to WAKE's (1993) interpretations. However, the presence of a similar morphotype in *Arthroleptis*, a non-excavating anuran, would falsify the hypothesis that intends to explain these morphologies as a function of a particular habit.

Nevertheless, there is a structural base of the muscle determined by its function as a mouth-opener. As the m. *depressor mandibulae* opens the mouth, it must originate and insert in areas where this function is possible. The variations in the muscle shape, possibly determined by epigenetic factors, would be related to the switch from aquatic to terrestrial life habits. The remarkable consistency of this muscle in saurians and ophidians (Moro & Abdala, personal communication) allows us an epigenetic interpretation for the anatomic variability in anurans. However, the epigenetic action has constraints. For example: *Gastrotheca gracilis*, *G. chrysosticta* and *G. christiani* have different developments, direct and with tadpole larvae, needing very different environments to develop. However, and despite of variable epigenetic pressures on the different species mentioned, the m. *depressor mandibulae* morphology is exactly the same in all of them. Changes during early development of the jaw muscles with little or no effect on the adult morphology have been described previously for direct developing frogs (*Eleutherodactylus coqui*, by HANKEN et al., 1997).

Likewise, the presence of the same *depressor mandibulae* muscle structure in anurans with different diets (STARRETT, 1968) does not agree with EMERSON's (1985) idea about m. *depressor mandibulae* shape being directly related to feeding habits, which limits its action as an epigenetic factor

## CONCLUSIONS

The morphology of the m. *depressor mandibulae* is too variable to be of much use in determining relationships or indicating habitat specializations. This variability seems to represent the most remarkable characteristic of this muscle.

In spite of the extreme variability of this muscle, we recognize some morphotypes that are useful to characterize some groups. They allow the use of the m. *depressor mandibulae* pattern as one character to be used in phylogenetic hypotheses including those groups.

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Source : MNHN, Paris

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Source : MNHN, Paris

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Source : MNHN, Paris

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## APPENDIX 1

## MATERIAL ANALYSED

FAMILY DISCOGLOSSIDAE
*Alytes obstetricans* (1). – FML 02782.

FAMILY PIPIDAE
Dactylethrinae
*Xenopus laevis* (2). – FML 03162.
*Hymenochirus boettgeri camerunensis* (1). – FML 03113.

FAMILY BUFONIDAE
*Bufo arenarum* (7). – FML 00540, 04722.
*Bufo granulosus major* (5). – FML 01052, 04224.
*Bufo paracnemis* (2). – FML 02168, 00364.
*Bufo spinulosus* (4). – FML 00759.
*Melanophryniscus rubriventris rubriventris* (8). – FML 02502, 02116.

FAMILY LEPTODACTYLIDAE
Ceratophryinae
*Ceratophrys cranwelli* (3). – FML 0492.
*Chacophrys pierottii* (2). – FML 01020.
*Lepidobatrachus llanensis* (3). – FML 01095, 05290, 08902.
Hylodinae
*Crossodactylus gaudichaudii* (1). – FML 03497.
Leptodactylinae
*Leptodactylus bufonius* (5). – FML 04642, 05364.
*Leptodactylus chaquensis* (4). – FML 05490, 05111.
*Physalaemus biligonigerus* (10). – FML 05288, 05986.
*Pleurodema borellii* (6). – FML 01377, 02694.
*Pseudopaludicola boliviana* (7). – FML 04307, 04309.
Telmatobiinae
*Alsodes* sp. (2). – FML 04435.
*Batrachyla* sp. (1). – FML 03713.
*Hylorina sylvatica* (1). – FML 03910.
*Telmatobius laticeps* (3). – FML 03960.
*Telmatobius oxycephalus* (3). – FML 02529.
*Telmatobius scrocchii* (3). – FML 05772.

FAMILY MYOBATRACHIDAE
Myobatrachinae
*Crinia georgiana* (1). – DIAM 015.
*Taudactylus diurnus* (1). – FML 03774.
*Uperoleia aspera* (1). – DIAM 017.
*Uperoleia borealis* (1). – DIAM 016.
Limnodynastinae
*Limnodynastes dumerili* (1). – DIAM 011.
*Limnodynastes convexiusculus* (1). – DIAM 012.

Source : MNHN, Paris

*Limnodynastes dorsalis* (1). – DIAM 008
*Limnodynastes fletcheri* (1). – DIAM 009
*Limnodynastes ornatus* (1) – DIAM 010
*Notaden melanoscaphus* (16). – FML 03783, DIAM 013.
*Notaden nichollsi* (1). – DIAM 014.

FAMILY RHINODERMATIDAE
*Rhinoderma darwinii* (4) – FML 03694

FAMILY HYLIDAE
Hemiphractinae
*Gastrotheca gracilis* (6). – FML 01769, 02209.
*Gastrotheca christiani* (2 adults and 3 juveniles) – FML 02117, 02918
*Gastrotheca chrysosticta* (2). – FML 02759.
Hylinae
*Acris crepitans* (1). – FML 09478.
*Argenteohyla siemersii* (4). – FML 00056
*Hyla andina* (3). – FML 04758, 00698
*Hyla boans* (1). – RL 105039, FML 09543.
*Phrynohyas venulosa* (3). – FML 02303, 02712.
*Plectrohyla guatemalensis* (1). – RL 64105.
*Ptychohyla ignicolor* (1) – RL 137222
*Scinax fuscovarius* (4). – FML 04635, 02716, 02754
*Smilisca sila* (1) – RL 918887
Phyllomedusinae
*Agalychnis saltator* (1). – FML 09541.
*Phyllomedusa boliviana* (4). – FML 01345, 02706.
*Phyllomedusa hypocondrialis* (4). – FML 01483, 04286
*Phyllomedusa sauvagii* (4). – FML 04899

FAMILY CENTROLENIDAE
*Centrolene grandisonae* (1). – FML 04980.
*Cochranella ignota* (3). – FML 04965, UVC 12091.

FAMILY PSEUDIDAE
*Lysapsus limellus* (3). – FML 04341, 00791.
*Pseudis minutus* (3) – FML 03676.
*Pseudis paradoxus* (6). – FML 00708, 04661, 00936.

FAMILY MICROHYLIDAE
Brevicipitinae
*Breviceps poweri* (1). – FML 03165
Microhylinae
*Dermatonotus muelleri* (5). – FML 05365, 01074.
*Elachistocleis bicolor* (7). – FML 00251, 00151, DIAM 029
Phrynomerinae
*Phrynomantis bifasciatus* (1). – FML 03029

FAMILY DENDROBATIDAE
*Colostethus subpunctatus* (1). – FML 02598
*Dendrobates auratus* (1) – FML 01722.
*Epipedobates pictus* (1). – FML 03516

FAMILY HEMISOTIDAE
*Hemisus guineensis guineensis* (3). – FML 01244

Source : MNHN, Paris

FAMILY ARTHROLEPTIDAE
Arthroleptinae
*Arthroleptis stenodactylus stenodactylus* (1). – FML 00066.
*Arthroleptis tuberosus* (2). – FML 00051.
*Cardioglossa cyaneospila* (1) – FML 06477.
*Schoutedenella* sp. (1). – RL Lote 24.
*Schoutedenella sylvatica* (1). – RL Lote 231.

FAMILY RANIDAE
Dicroglossinae
*Conraua crassipes* (2). – FML 03068.
*Hoplobatrachus occipitalis* (1). – No data
Ptychadeninae
*Ptychadena mascareniensis hylaea* (3). – FML 01228.
Pyxicephalinae
*Aubria subsigillata* (1). – FML 03154
Raninae
*Rana albolabris* (2). – Lote 231.
*Rana angolensis* (3). – FML 03188.
*Rana lepus* (1). – RL Lote 231.

FAMILY PETROPEDETIDAE
*Phrynobatrachus calcaratus* (2). – RL Lote 231
*Phrynobatrachus acutirostris* (1) – DIAM 006

FAMILY HYPEROLIIDAE
Hyperoliinae
*Afrixalus orophilus* (4). – FML 03229, 03230.
*Chrysobatrachus cupreonitens* (3). – FML 02081.
Kassininae
*Kassina senegalensis angeli* (2). – FML 02076.
Leptopelinae
*Leptopelis notatus* (2). – FML 03205

FAMILY RHINOPHRYNIDAE
*Rhinophrynus dorsalis* (1). – FML 01720.

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Source : MNHN, Paris

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# The tadpole of *Phrynobatrachus mababiensis* FitzSimons, 1932 (Anura, Ranidae, Petropedetinae)

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**The tadpole of the poorly known puddle frog *Phrynobatrachus mababiensis* FitzSimons, 1932 from Eastern Africa is described and illustrated.**

## INTRODUCTION

The puddle frog genus *Phrynobatrachus* Günther, 1862 comprises about 64 currently recognized species (FROST, 1985) Of these, only the tadpoles of *P natalensis* (Smith, 1849) (POWER, 1927, CHANNING, 2001), *P guineensis* Guibé & Lamotte, 1961 (RODEL, 1998) and *P alticola* Guibé & Lamotte, 1961 (RÖDEL & ERNST, 2002) have been described. *Phrynobatrachus mababiensis* FitzSimons, 1932 (Dwarf Puddle frog, WAGER, 1986, Mababe River frog, FRANK & RAMUS, 1996) is a small frog that usually calls from low in thick vegetation on flooded terrains close to the water Very little has been published about the biology of this species PASSMORE & CARRUTHERS (1979) reported the advertisement call of *P mababiensis*, and WAGER (1986) provided a few comments about the tadpole (see discussion below) Herein we describe the tadpole of *Phrynobatrachus mababiensis*

## MATERIAL AND METHODS

Tadpoles of *Phrynobatrachus mababiensis* (34 individuals) were collected at Kibebe Farm (08°29'0.5"S, 35°08'50 3"E), Iringa, Tanzania, by the authors on 8 February, 2000. Specimens were fixed in 10 % formalin (commercial grade) at the time of collecting them One tadpole was at developmental stage 30 (GOSNER, 1960), whereas the remaining tadpoles were at developmental stage 26 or earlier These specimens were deposited at the National Museum of Natural History, Smithsonian Institution, Washington, USA (USNM 539462-82)

Source : MNHN, Paris

Species identification was based on comparisons of our material with specimens collected by A. Channing on 12 January, 1986, at Katima Mulilo, Caprivi Region, Namibia (17°38'00"S, 24°11'00"E), in a shallow, muddy pool with grasses. The tadpoles collected in Iringa, Tanzania, are identical to those from Katima Mulilo, Namibia. Of the three tadpoles collected at Katima Mulilo, one was preserved whereas the other two were raised to juveniles for identification purposes, and they correspond to *P. mababiensis*. These specimens were deposited at the Transvaal Museum, Pretoria, South Africa (TM 83618). The Katima Mulilo specimens are the closest material available to the type locality, Katima Mulilo is about 120 km north of the type locality of *P. mababiensis* in the Mababe Depression, NW Botswana.

Specimens were staged according to GOSNER (1960). The labial tooth row formula is given according to ALTIG (1970). Terminology of measurements taken follows ALTIG & MCDIARMID (1999). Measurements (in millimeters) were made using a Mitutoyo digital calliper and are based on specimens ($n$ = 19) at Gosner stage 26 (USNM 539462-539480). Means and standard deviations are given in the description (see tab. 1). The tadpole illustration is based on specimen USNM 539481 (Gosner stage 30), the most advanced stage available in our sample.

## RESULTS AND DISCUSSION

### TADPOLE DESCRIPTION

Tadpoles of *Phrynobatrachus mababiensis* have a depressed and elliptical body (fig. 1). In dorsal and lateral views the snout is rounded, in lateral view the snout slopes gradually anteriorly toward the oral disc. The eyes are large and lateral. The external nares are located half way between the eyes and the tip of the snout. The narial aperture is small, rounded, and laterodorsally positioned. Tail fins are low, dorsal and ventral fins almost parallel the tail musculature and are of approximately equal height. The dorsal fin originates at the tail-body junction and the ventral fin originates at the posterior ventral terminus of the body. Tail fins slope gradually posteriorly to a narrowly rounded tip. The tail musculature extends to the tip of the tail. The spiracle is sinistral with a midlateral opening directed dorsally. The vent tube and aperture is dextrally placed relative to the ventral fin. Measurements of the illustrated tadpole (USNM 539481) at Gosner stage 30 are: TL 17.2, BL 5.9, MTH 2.2; TMW 1.0, E 0.8, IOD 2.6. Measurements and summary statistics of additional 19 tadpoles at developmental stage 26 are given in table 1.

The oral disc is anteroventrally positioned, emarginate, and has a uniserial row of conical papillae with rounded tips (fig. 2). The row of marginal papillae has a large dorsal gap occupying most of the upper labium. In addition, two pairs of long papillae project from the lower labium, posterior to the marginal papillae. These are about 2-3 longer than the marginal papillae. A few submarginal papillae are found laterally on the upper labium. The labial tooth row formula is 4(2-4)/4(1). Upper and lower jaw sheaths are wide, pigmented for about one third of their width, and have widely serrated edges.

Source : MNHN, Paris

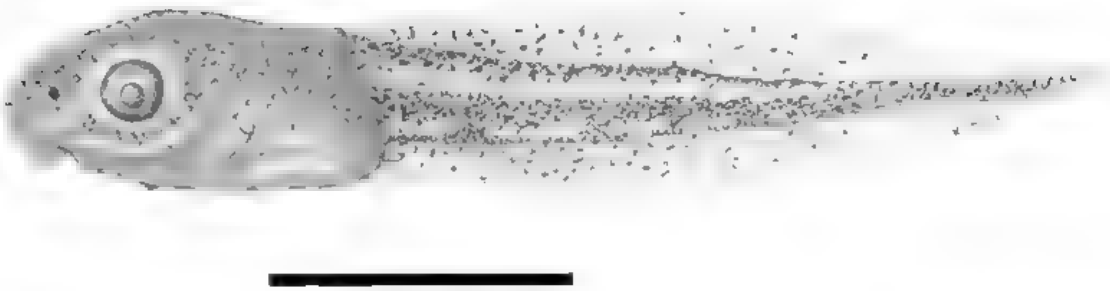

Fig. 1 — Tadpole of *Phrynobatrachus mababiensis* FitzSimons, 1932, stage 30, USNM 539481. Bar: 5.0 mm.

Table 1. — Measurements (in mm) of 19 tadpoles of *Phrynobatrachus mababiensis* FitzSimons, 1932. TL, total length; BL, body length; MTH, maximum tail height; TMW, tail muscle width; E, eye diameter; IOD, interorbital distance.

| USNM number | TL | BL | MTH | TMW | E | IOD |
|---|---|---|---|---|---|---|
| 539462 | 17.1 | 6.0 | 2.4 | 0.9 | 0.8 | 2.7 |
| 539463 | 18.2 | 6.8 | 3.2 | 1.3 | 0.9 | 2.9 |
| 539464 | 16.2 | 5.7 | 3.4 | 1.0 | 1.0 | 2.5 |
| 539465 | 15.9 | 5.9 | 2.9 | 1.0 | 1.0 | 2.5 |
| 539466 | 16.0 | 6.1 | 3.2 | 1.1 | 1.0 | 2.9 |
| 539467 | 16.3 | 5.9 | 2.6 | 0.9 | 0.8 | 2.7 |
| 539468 | 16.4 | 6.1 | 2.8 | 1.0 | 1.0 | 2.6 |
| 539469 | 16.3 | 5.8 | 3.4 | 1.1 | 0.8 | 2.4 |
| 539470 | 15.4 | 6.2 | 2.8 | 1.1 | 1.0 | 2.7 |
| 539471 | 16.2 | 5.8 | 3.6 | 1.1 | 0.8 | 2.3 |
| 539472 | 16.8 | 5.9 | 3.0 | 1.1 | 1.0 | 2.4 |
| 539473 | 17.4 | 5.9 | 3.5 | 1.2 | 0.9 | 2.7 |
| 539474 | 16.4 | 5.8 | 3.6 | 1.1 | 0.9 | 2.7 |
| 539475 | 16.3 | 5.6 | 3.2 | 1.2 | 0.9 | 2.4 |
| 539476 | 16.6 | 5.7 | 2.9 | 0.9 | 0.8 | 2.5 |
| 539477 | 16.0 | 5.8 | 3.2 | 1.0 | 0.8 | 2.7 |
| 539478 | 15.1 | 5.5 | 2.8 | 1.1 | 0.8 | 2.8 |
| 539479 | 16.2 | 5.6 | 2.9 | 1.2 | 0.9 | 2.5 |
| 539480 | 16.6 | 5.8 | 2.7 | 1.0 | 0.9 | 2.2 |
| Mean | 16.40 | 5.88 | 3.06 | 1.07 | 0.89 | 2.59 |
| Standard deviation | 0.68 | 0.30 | 0.34 | 0.10 | 0.06 | 0.19 |

Source : MNHN, Paris

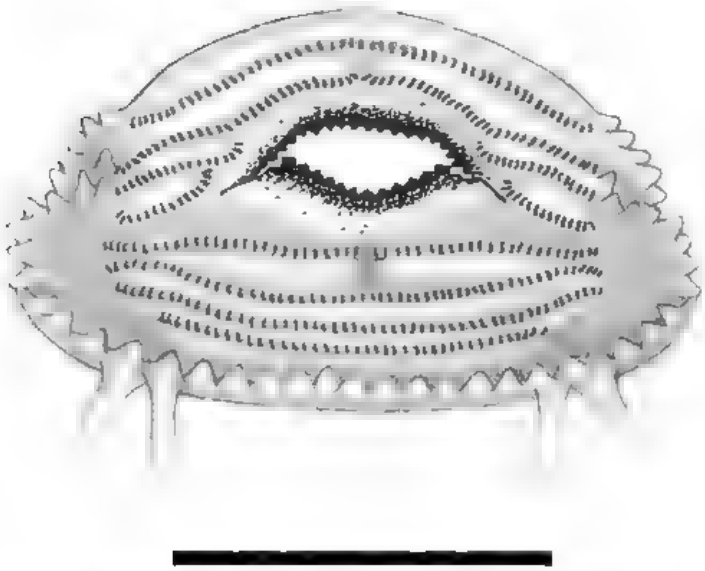

Fig. 2 Oral disk of *Phrynobatrachus mababiensis* FitzSimons, 1932, stage 30, USNM 539481. Bar 1.0 mm

In preservative, specimens are dark brown. The fins and tail musculature are speckled with dark melanophores. These melanophores are more dense on the dorsal and ventral edges of the tail musculature, melanophores also are dense along and immediately below the main axis of the tail musculature. Visually, this accumulation of melanophores outlines a distinct, pale, whitish band that extends along the epaxial muscles for about two thirds of the tail. A second, but shorter and less distinct, band is present on the hypaxial muscles. The posterior third of the tail musculature is homogeneously dark and the myotomes are poorly defined. Melanophores are abundant on the dorsal and lateral surfaces of the body where they are homogeneously distributed, ventrally they are present only on the anterior half of the body.

## TADPOLE COMPARISONS

WAGER (1986) provided greatly oversimplified descriptions, including outline illustrations, of tadpoles of *Phrynobatrachus mababiensis* and *P. natalensis*. These descriptions do not agree with the previously reported tadpole of *P. natalensis* (POWER, 1927) nor with the present description of *P. mababiensis*.

WAGER (1986) reported the oral disk of *P. mababiensis* as having a labial tooth row formula of 1/2 and possessing a double row of marginal papillae in the lower labium, with the outer row consisting of elongated papillae. CHANNING (2001) included Wager's description in his section of tadpoles. A row of elongated papillae on the lower labium for early stages (total length 6.0 mm) of *P. natalensis* was reported by POWER (1927). It is possible that WAGER (1986) may have misidentified the larvae, alternatively, a row of long papillae on the lower row may be present in early stages of *P. mababiensis*, however we have not seen it.

Source : MNHN, Paris

In contrast to those of *P mababiensis*, the tadpoles of *Phrynobatrachus guineensis* and *P alticola* (Rödel, 1998; Rödel & Ernst, 2002) have morphological characteristics and modifications typical of phytotelmic anuran larvae.

## Acknowledgments

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*Corresponding editor:* W. Ronald Heyer

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Source : MNHN, Paris

# Notes on the treefrogs (Hyperoliidae) of North-Western province, Zambia

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**This paper is based on a collection of treefrogs (Hyperoliidae) from northern Mwinilunga district, North-Western Zambia. *Hyperolius cinnamomeoventris* is new to Zambia, *Hyperolius kivuensis* and the doubtful *Leptopelis parbocagii* are additions for the district. *Hyperolius nasutus* and *Hyperolius benguellensis* are established as separate species based on distinct structures of their calls. *Hyperolius bocagei* is established as a synonym of a member of the *Hyperolius viridiflavus* superspecies.**

## INTRODUCTION

Northern Mwinilunga district in the North-Western province of Zambia stretches as a peninsula between Angola and République Démocratique du Congo, countries where biological fieldwork is difficult. This part of Zambia has therefore received considerable attention from herpetologists, and the fauna of Amphibia is reasonably well known (for treefrogs, see: SCHIØTZ, 1975, 1999, POYNTON & BROADLEY, 1987; BROADLEY, 1991).

The present note is based on a collection made by the authors during a brief stay in the district, 11 days in November 1999. The following localities were visited (1) 2-5.11.1999, Hillwood farm (11°15'S, 24°18'E); (2) 5-6.11.1999, Zambesi rapids (11°08'S, 24°08'E), (3) 6-9.11.1999, Jimbe river (10°57'S, 24°07'E), (4) 9-11.11.1999, Kachifiwiru (10°57'S, 24°06'E).

Although before the onset of the heavy rains, it was possible to secure or observe probably all the species that have been reported from the area, with two additions to the district and one to the country. This note thus covers all species of Hyperoliidae which have been recorded from the Mwinilunga district. Only information regarded as new is given in this paper. POYNTON & BROADLEY (1987) and SCHIØTZ (1975, 1999) gave a more general treatment. The preserved material is deposited in the Zoological Museum, Copenhagen (ZMUC).

Source : MNHN, Paris

## TAXONOMY

### **Afrixalus wittei** (Laurent, 1941)

*Comments.* – Abundant and conspicuous in savanna localities. All collected specimens have an identical pattern.

*Material.* – Fishpond near Jimbe river. ZMUC R 077939-40, R.077999 (2 ♂, 1 ♀); Hillwood: ZMUC R.076676-77, R.076696, R 077926-38 (16 ♂).

### **Hyperolius nasutus** Günther, 1864

*Comments.* – See remarks under *Hyperolius benguellensis*. Sixteen of the specimens (ZMUC R.77957-72) were collected when calling and could therefore be distinguished with absolute certainty from *H. benguellensis* by the voice. The remaining material is from the same ponds, where no *H. benguellensis* were heard.

*Voice.* – A brief scream, apparently similar to the voice of this species elsewhere in its vast range (fig. 1).

*Material.* – "Paul's Fishpond", Hillwood. ZMUC R.077957-83 (25 ♂, 2 ♀).

### **Hyperolius benguellensis** (Bocage, 1893)

*Comments.* – The possible occurrence of a species very similar to, but distinct from, *Hyperolius nasutus* in southern Africa has long been discussed. SCHIØTZ (1975) recognised with doubt the species *Hyperolius granulatus* (Boulenger, 1901) and so did, with similar doubt, POYNTON & BROADLEY (1987) although they used the older name *H. benguellensis*, whereas SCHIOTZ (1999) reluctlantly lumped *H. nasutus* with *H. benguellensis*.

During our field studies, we observed two structurally different voices in the study area. The two types of calls were not heard from the same breeding localities, but from localities only a few hundred meters apart.

We believe that the two call types represent two different species and that our separation of the material between the species *H. benguellensis* and *H. nasutus* is correct, also for the specimens not heard calling when collected since we spent several nights collecting in the localities and listened especially for aberrant voices. Many voices were heard, but none belonging to *H. nasutus* at a *H. benguellensis* locality or vice versa.

POYNTON & BROADLEY's (1987) meticulous discussion of the *H. benguellensis-nasutus* group is based on the assumption that the paravertebral lines are the key characters for *H. benguellensis*. However, of our material of this species, out of 41 specimens only 6 show paravertebral lines after preservation. We are therefore not confident that POYNTON & BROADLEY's (1987) distinction between the two species is congruent with ours.

If samples are separated according to the voices it is possible to differentiate the two species on external morphology. In mixed, preserved samples we believe that not all specimens

Source : MNHN, Paris

Fig. 1 – Voice of *Hyperolius nasutus*, Hillwood. The horizontal lines are 1kHz apart, the marks on the horizontal axis are 0 1 sec. apart

can be identified with certainty The extent of webbing seems to be the best character, although the webbing of *H nasutus* varies so much over its range that this character must be treated with caution and may be valid only in this part of Africa. The dorsal skin may be more coarsely granulated in *H. benguellensis*, but the difference is not great (see tab 1).

Table 1. Comparison between *Hyperolius nasutus* Günther, 1864 and *Hyperolius benguellensis* (Bocage, 1893).

| *Hyperolius nasutus* | *Hyperolius benguellensis* |
|---|---|
| Characters in life | |
| Translucent green | Often darker green |
| No paravertebral lines | Sometimes paravertebral lines |
| Sometimes fine middorsal line | No middorsal line |
| Voice a scream | Voice a brief rattle |
| Characters after preservation | |
| Ground colour lighter | Ground colour darker |
| Nares less protruding | Nares more protruding |
| More webbing | Less webbing |
| Dorsum finely granulated | Dorsum more coarsely granulated |

Source : MNHN, Paris

WILSON (in press) discovered a degeneration in the tympanic apparatus in *H. benguellensis*, a character not found in *H. nasutus*. She kindly examined our material of both species and found the difference in tympanum consistent with our separation.

In spite of the degeneration of the tympanic apparatus, the presence of a voice seems to imply that *H. benguellensis* is not deaf. HETHERINGTON & LINDQUIST (1999) pointed at alternative hearing mechanisms.

*H. benguellensis* is similar in colour pattern to *Hyperolius viridis* Schiøtz, 1975 from south-western Tanzania. *H. viridis* is, however, a larger frog (male snout-vent length 22-26 mm vs. 17-22 mm in *H. benguellensis*) and especially a much more massive, broader frog, similar in body proportions to the smaller *Hyperolius pusillus* (Cope, 1862).

*Colour in life.* – Translucent green, sometimes darker, more "dense" green. Many specimens have a pair of light dorsolateral lines, and an additional, more diffuse pair of paravertebral lines (fig. 3a). Other specimens lack the paravertebral lines, and some also lack the dorsolateral lines and have diffuse dark spots on dorsum (fig. 3b). The latter two morphs seem inseparable in pattern from *H. nasutus*, although they are sometimes somewhat darker.

*Breeding.* – The eggs have a white and a dark greenish pole.

*Voice.* – A brief rattle, acoustically quite distinct from the voice of *H. nasutus*. The sonogram (fig. 2) shows a brief series of rather indistinct figures at 4000-4200 Hz. The voice illustrated in SCHIØTZ (1975: fig. 96) from Kabwe (Zambia) as that of *H. nasutus* is in fact that of *H. benguellensis*.

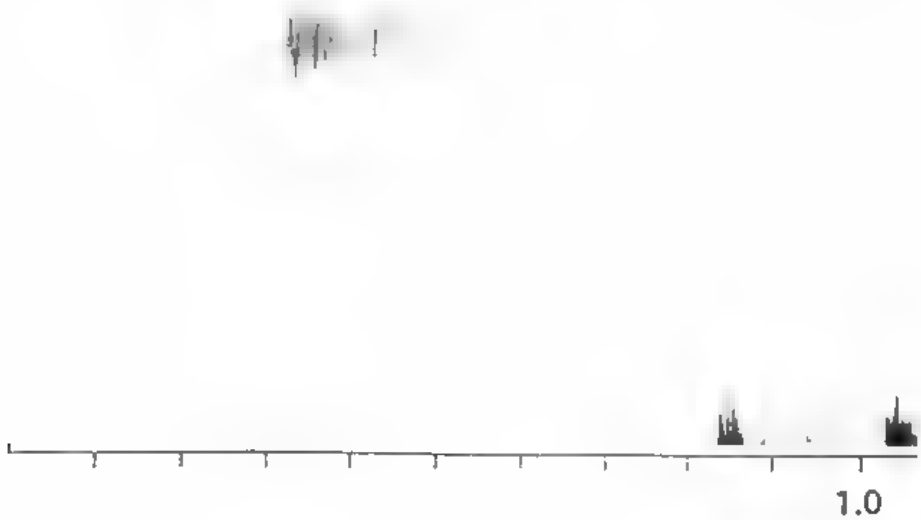


Fig. 2. Voice of *Hyperolius benguellensis*, Hillwood

Source : MNHN, Paris

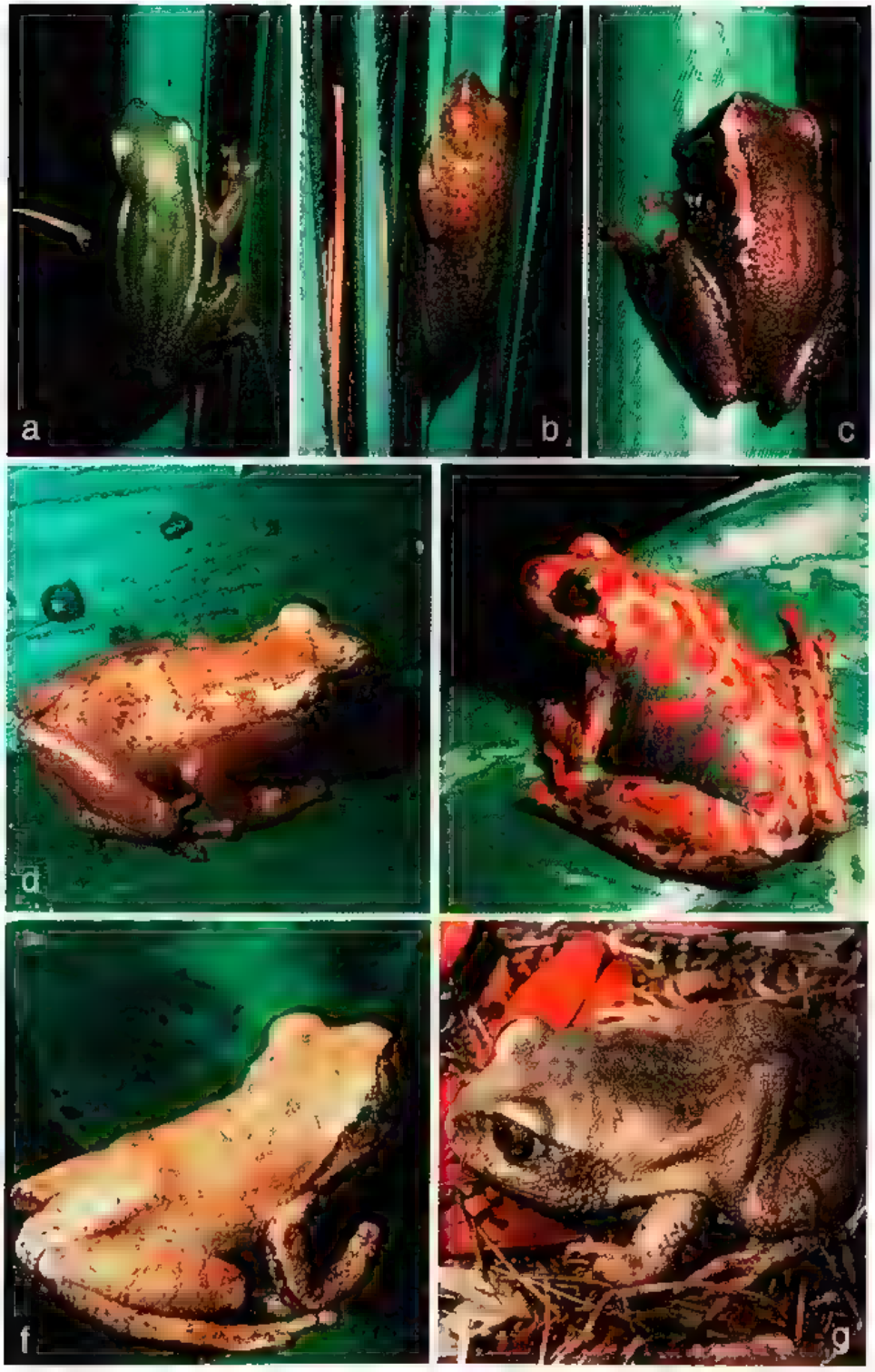


Fig. 3. (a–b) *Hyperolius benguellensis*, Hillwood. (a) specimen with paravertebral lines, (b) spotted morph. (c–d) *Hyperolius major*, Kachitwiru. (c) phase 2, (d) phase 1. (e) *Hyperolius parallelus albomitus*, ♀, Hillwood. (f) *Leptopelis cinnamomeus*, ♂, Zambesi rapids. (g) *Leptopelis parbocagii*, ♂, Zambesi rapids.

Source : MNHN, Paris

Only few calling populations of *H. nasutus* and *H. benguellensis* were heard, so no conclusions in relation to habitat preference could be drawn The two species were not heard at the same localities. While *H. nasutus* was heard in old, partly overgrown fishponds with much low vegetation. *H. benguellensis* was taken in more open water holes on the grass-covered plains at Hillwood These last localities would seem to be similar to localities with *H nasutus* from other places in Africa.

Of the present material, 10 males were taken when calling (ZMUC R.076709-18).

*Material.* – Hillwood: ZMUC R 076709-49 (35 ♂, 6 ♀)

**Hyperolius quinquevittatus** Bocage, 1866

*Comments* No breeding activity was observed. The specimens were taken by chance far from water Some of the specimens have a pattern which differs somewhat from that hitherto recorded for the species in life dorsum brown with three conspicuous golden-green bands (i e a middorsal and two lateral bands), delimited with dark brown lines. Although it is in principle the same pattern as e g that shown in SCHIOTZ (1999: fig. 175), the general impression is that of a dark frog with 3 light stripes.

*Material.* Kachifwiru: ZMUC R.771016-19 (4 ♂); Hillwood: AMUC R.076707, R.771104-05 (2 ♀, 1 juvenile); Zambesi rapids: ZMUC R 076750 (1 juvenile).

**Hyperolius kivuensis** Ahl, 1931

*Comments.* – Only a single male collected.
*Material.* – Kachifwiru: ZMUC R.0771015 (1 ♂).

**Hyperolius parallelus alborufus** Laurent 1964

*Comments.* A member of the *Hyperolius viridiflavus* superspecies. The species structure within this group is unsettled and disputed The present form is conventionally included in the species *Hyperolius marmoratus* Rapp 1842, whereas SCHIOTZ (1971, 1975) has argued for its inclusion in the species *Hyperolius parallelus* Günther, 1859.

The type series from Cazombo (Angola) has black dots round the anus and on the tarsi Such spots are absent in the present sample The form *alborufus* is very similar to other forms in the very variable complex from this part of Africa, and a detailed study of the variation would seem rewarding

The present collection shows great uniformity in pattern as all specimens of the female phase have the pattern shown in figure 3e. It is remarkable that a sample collected by Ronalda Keith, also from the Mwimilunga district, shows much variation in pattern (see SCHIOTZ, 1971: fig 13, 1975 fig. 181, 1999, fig 474a-e) This may be due to selective collection by Keith Our sample was collected without any bias as to pattern. Also the sample reported in BROADLEY (1991) shows little variation (Broadley, in lit.).

Source : MNHN, Paris

Breeding activities had hardly started during our visit, and only a few males were calling from the ponds. There was, however, quite a number of males calling widely scattered in the rather dense Miombo woodland in the area, apparently while migrating towards water. The voice emitted here was the coarse "initial sound" and only a few times was the melodic breeding call heard. Males and females collected there and kept in plastic bags did not produce eggs during the night, something that would always happen if collected on the breeding site.

*Colour in life* – In life, all phase F specimens had a bright red vermiculation on a light, greyish background. Females had a bright red ventrum and conspicuously blue subdermal lateral band (for explanation of this term, see SCHIØTZ, 1999: 199). The males of phase F were similar, but with a less conspicuous subdermal lateral band. Males of phase J were brown with a darker hour-glass pattern.

*Material* – Fishpond near Jimbe river: ZMUC R.771000-03, R 771045-47 (6 ♂, 1 ♀), Hillwood: ZMUC R.076683-95 (10 ♂, 3 ♀).

**Hyperolius major** Laurent, 1957

*Comments* – Described as a subspecies of *Hyperolius platyceps* (Boulenger 1900) but regarded as a full species by SCHIØTZ (1975), mainly because the status of the name *H. platyceps* was unclear. *H. platyceps* has later been defined (AMIET, 1978; SCHIØTZ, 1999). In morphology and pattern, the present taxon is very similar to *H. platyceps* from north-western Central Africa. It is here regarded as a full species because the voice differs from that of *H. platyceps*.

*Colour in life* – Two phases. Phase 1: dorsum light brown with a darker hour-glass pattern; very dark loreal area, continuing behind the eye, the light pattern forming a triangle on the snout (fig. 3d). Phase 2 (presumed female phase): dorsum uniform brown with light canthal and dorsolateral stripe, also extending over upper eyelid (fig. 3c). Both phases: arms and legs dark brown, in some specimens with conspicuous small light spots. Many specimens have similar light spots in the dark pattern. Ventrum and throat orange. Ventral side of limbs darker orange. The single female collected is of phase 2, brown with a lighter brown lateral stripe.

*Breeding* – Found exclusively in the dense gallery forests, thus being a "farmbush form" or "bushland form" according to the terminology of Schiøtz, collected together with *Leptopelis cynnamomeus* (Bocage, 1893).

The eggs have a white and a black pole.

*Voice* – An initial coarse creak, followed by a series of hard, unmelodic clacks in rapid succession, almost *Afrixalus*-like (fig. 4). Such a vocal structure, with elements in a measured rhythm, is quite unusual in the genus, found in *Hyperolius guttulatus* Günther, 1859, *Hyperolius tuberculatus* Mocquard, 1897, *Hyperolius pseudargus* Schiøtz & Westergaard, 1999 and a few others. The sonogram of *H. major* in SCHIØTZ (1999, fig. 400) is of the initial creak.

*Material* – Kachifwiru: ZMUC R 771025-37 (12 ♂, 1 ♀); Jimbe river: ZMUC R.771038-44 (7 ♂).

Source : MNHN, Paris

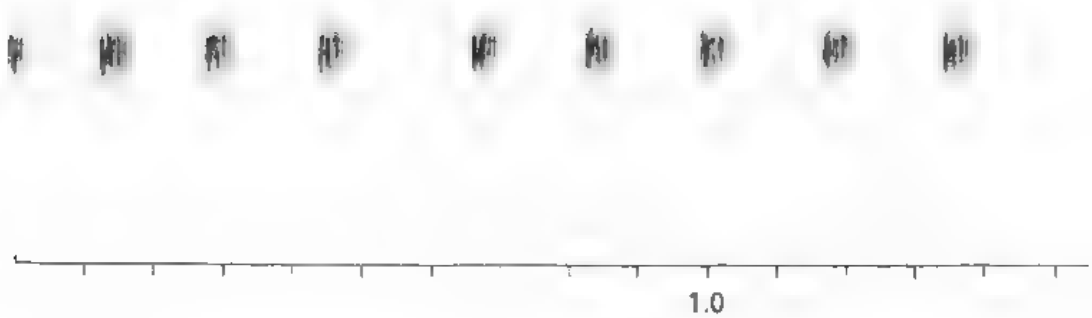


Fig. 4. – Voice of *Hyperolius major*, Kachifwiru.

**Hyperolius kachalolae** Schiøtz, 1975

*Comments.* The present samples differ somewhat from the small sample from the type locality After preservation they have a more baggy, often pigmented gular sac, and in life the sac is yellow to black, not turquoise as in the types. Nevertheless we are convinced that the specimens listed here are conspecific with *H. kachalolae* The voice is the same, and the thin red canthal- and dorsolateral lines seem diagnostic.

One of our samples (from granite outcrops near Zambesi rapids) differed in life somewhat from the other samples, mainly in the absence in most specimens of red canthal and dorsolateral lines, and with a large proportion of the males being very dark and with a black gular sac We were in doubt as to whether two species were involved, but after preservation is it impossible to distinguish that sample from the rest as especially the lighter specimens show red canthal and dorsolateral lines, sometimes very faint, also the voice is identical to that of the other samples of *H. kachalolae*.

Poynton & Broadley (1987) expressed doubt as to whether *H. kachalolae* is different from *Hyperolius bocagei* Steindachner, 1867 The senior author has examined the holotype of *H. bocagei* (Naturhistorisches Museum Wien, NMW 14846), a surprisingly well preserved, large female (35.1 mm) with a well-developed gular fold and extensive webbing These characters, and the white, "chalky" dorsal surfaces, make it certain that it is a member of the *Hyperolius viridiflavus* superspecies as suggested in Schiøtz (1999) Neither the imprecise type locality (Angola) nor the pattern of the type (chalky white, as normal in the dry season) permit reference to a specific subspecies in the complicated *H. viridiflavus-marmoratus-parallelus* group, so no nomenclatorial change based on priority seems necessary

Source : MNHN, Paris

*H. bocagei* has been recorded from a number of localities in Angola, southern R. D. Congo and northern Zambia, and *H. kachalolae* so far only from the type locality. Since *H. kachalolae* is abundant and very conspicuous in the Mwinilunga district – in fact the dominant *Hyperolius* –, it seems unlikely that it has not been collected in neighbouring Angola and southern R. D. Congo, nor being found in the material referred to as *H. bocagei* in POYNTON & BROADLEY (1987). According to the description especially the last could well be *H. kachalolae*. There are some samples in museums of members of the *H. viridiflavus* group identified as *H. bocagei* by R. F. Laurent (see SCHIØTZ, 1999: 188).

In conclusion, *Hyperolius bocagei* is a synonym of one of the members of the *H. viridiflavus* superspecies whereas we believe that several later records of *H. bocagei* in the literature refer to *H. kachalolae*.

*Colour in life*. – Males: dorsum green to straw-coloured to black with red fingers and toes. Some populations have a conspicuous red canthal line, continuing behind the eye, often as spots. Many specimens in other populations lack the red lines in life. Gular sac in males from yellowish to black, the latter especially in the black-backed specimens.

Females bright orange (our observations) or tomato red (Channing & Drewes, in lit.). Some females have a feebly developed transversal gular fold.

*Material*. – Fishpond, Jimbe river: ZMUC R0.77948-52, R.771048-67 (15 ♂, 10 ♀). Zambesi rapids: ZMUC R.077953-57, R.077968-078003 (39 ♂, 1 ♀); Kachifwiru: ZMUC R.771020-24 (5 ♂); Hillwood: ZMUC R.076678-79, R.076697-706 (11 ♂, 1 ♀).

**Hyperolius cinnamomeoventris** Bocage, 1866

*Comments*. – First record from Zambia, but not unexpected in view of its range. No calling heard.

*Material*. – Hillwood: ZMUC R.771012-14 (2 ♂, 1 ♀).

**Kassina senegalensis** Duméril & Bibron, 1841

*Comments*. – All collected specimens belong to the strange spotted, rather large morph (see photo in SCHIØTZ (1999: fig. 508), except one with an almost unbroken dorsal line.

*Material*. – Zambesi rapids: ZMUC R.77986-91 (4 ♂, 2 ♀), Hillwood: ZMUC R.771009-11 (3 ♂); Jimbe river: ZMUC R.076665 (1 ♂).

**Kassina kuvangensis** (Monard, 1937)

*Comments*. – The characteristic voice, quite different from that of *K. senegalensis*, was heard at an overgrown fishpond at Hillwood. No specimens could be collected. We did not hear the two species of *Kassina* from the same locality.

Source : MNHN, Paris

**Kassinula wittei** Laurent, 1940

*Comments* This tiny frog was quite common on the soggy, grass-covered rocks near the Zambezi rapids, but it was difficult to track down.

*Material.* Granite flats, Zambesi rapids: ZMUC R 77984-85 (2 ♂).

**Leptopelis cynnamomeus** (Bocage, 1893)

*Comments.* - This species was suggested to be one of the "savanna screamers" in SCHIØTZ (1999), a somewhat flippant term for a group consisting of vicariating savanna forms with a similar morphology and a very characteristic voice, but rather different patterns. We believe that some members of this group (*Leptopelis concolor* Ahl, 1929; *Leptopelis argenteus* (Pfeffer, 1893); probably *Leptopelis broadleyi* Poynton, 1985) are closely related, probably at the subspecies level, but cannot maintain *L. cynnamomeus* as a member of this group. It is not a savanna form, but a bushland form It has feebly developed pectoral glands (absent in the other forms), and the voice is audibly different from them.

*Colour in life.* Golden brown with diffuse, darker transverse bands and a dark interorbital streak. Loreal area dark (fig. 3f).

*Voice.* Calling from leaves, often several meters up, in dense riverine (gallery) forests. Voice a scream followed by 2-3 quiet clacks ("*yun-clack-clack*"), sometimes clacks alone. See sonogram in SCHIØTZ (1999: fig. 681).

*Note* - In the distribution map of "the savanna screamers" in SCHIØTZ (1999: fig 672), the symbols for *L. argenteus* and *L. broadleyi* have unfortunately been switched

*Material* - Kachifwiru ZMUC R 77992-97 (5 ♂, 1 ♀), Zambesi rapids: ZMUC R 771004-08 (5 ♂); Jimbe River: ZMUC R.076666-75 (8 ♂, 2 juveniles).

**Leptopelis parbocagii** Poynton & Broadley, 1987

*Comments* - POYNTON & BROADLEY (1987) established the species *L. parbocagii* with hesitation, since the difference from *L. bocagii* (Gunther 1864) seems very small. Their key character is the broader head of *L. parbocagii*, expressed as the ratio interorbital distance vs. nostril-tympanum being greater than 36 %. We are indebted to J. C. Poynton for having examined our material and confirmed that it falls well within the definition of *parbocagii* (♀ 37,5 %, ♂ 39,1-47,6 %), but we agree with Poynton & Broadley that *L. parbocagii* may not be a species distinct from *L. bocagii*

*L. parbocagii* is so far unrecorded from this area *L. bocagii* is recorded from Isombo Stream (POYNTON & BROADLEY, 1987; BROADLEY, 1991) and Hillwood, (BROADLEY, 1991) We have examined the material reported in BROADLEY, 1991 (8 specimens from Hillwood, 1 from Isombo Stream) They seem to fall within the definition of *L. parbocagii*, with an interorbital distance vs. nostril-tympanum of 36,8-50,9 %.

Source : MNHN, Paris

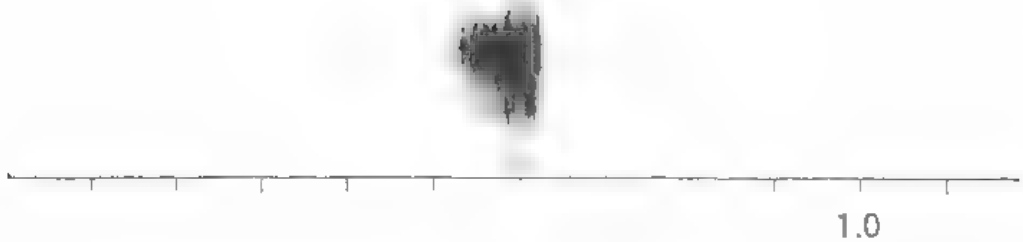


Fig. 5. – Mating call of *Leptopelis parbocagii*, Zambesi rapids.

All our specimens were taken in the savanna. The males from Jimbe River were calling in a cultivated field close to the gallery forest. Some males were calling from the ground, others from a low height in bushes.

*Colour in life.* - Dorsum grey to brown, often with a darker, almost black blotch on the dorsum (fig. 3g).

*Voice.* - A deep, atonal "*waab*", possibly indistinguishable from the voice of *L. bocagii* (fig. 5). As in several other *Leptopelis*, another call (territorial?) is sometimes heard, namely a long succession of clacks, almost inaudible at first but growing in intensity until the call ends with the usual clack. One such recorded call (fig. 6) has a total duration of 8 seconds.

*Material.* - Near Jimbe River: ZMUC R.77942-44 (5 ♂), Hillwood: ZMUC R.77945 (1 ♀), Kachifwiru: ZMUC R.77946-47 (2 ♂).

## ACKNOWLEDGEMENTS

The senior author is most indebted to the Carlsberg Foundation for its grant, making the tour possible. We are indebted to Robstein L. Chidavaenzi and D. G. Broadley for giving us the opportunity to examine their material of *Leptopelis parbocagii* and to F. Tiedemann for enabling us to examine the type of *Hyperolius bocagei*. We are furthermore indebted to our colleagues D. G. Broadley, A. Channing, R. C. Drewes, R. Stjernstedt, J. C. Poynton and Lindsay G. Wilson for comments and inspiring discussions.

Source : MNHN, Paris

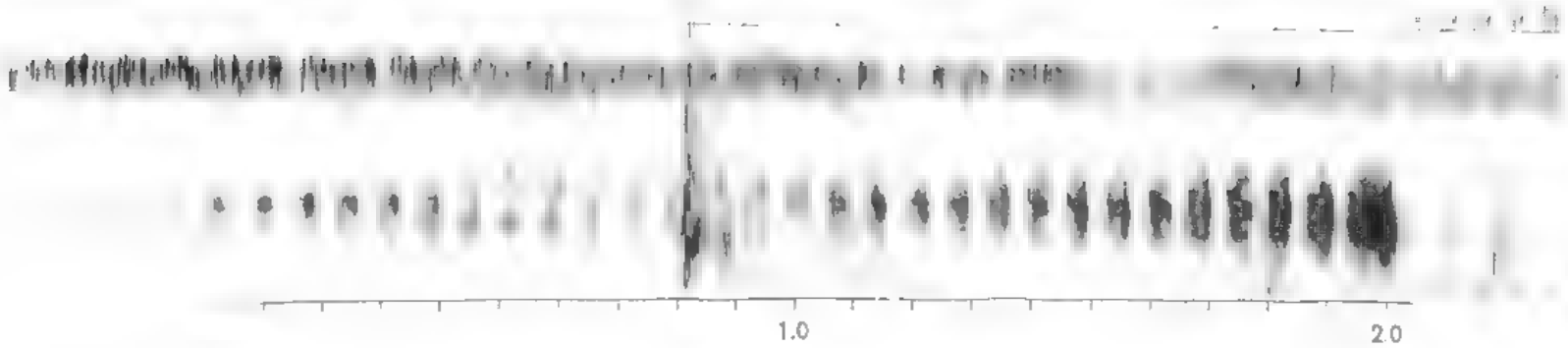


Fig 6 Presumed territorial call of *L. parbocagii*, Kachifwiru. Only the last 2 3 seconds of the call with a total duration of 8 seconds in shown. The call is the succession of figures with growing intensity seen between 1 and 2 kHz.

Source MNHN, Paris

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*Corresponding editor*: Alain DUBOIS



Source : MNHN, Paris

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# Diving behaviour of the Andean frog *Hyla labialis*

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**We describe the behaviour of *Hyla labialis* during descent, stationary phase and ascent of voluntary dives in a laboratory tank and in natural ponds. We compare dive times and activity of submerged frogs assigned to six categories established according to developmental stage, gender and reproductive state. In general, the descent took 1.6 % of the total dive time and contained 25 % of the total number of moves per dive, the stationary phase lasted 60.1 % of the total dive time and contained 12.5 % of the moves, and the ascent lasted 38.4 % of the total dive time, with 62.5 % of the moves. The longer the dive, the more moves did a frog make. Among adults, neither gender nor reproductive state was associated with differences in dive time or activity. Juvenile frogs had significantly shorter dive times than adults. The average dive time was significantly longer in a natural pond than in a laboratory tank. Individuals with longer dive times in the laboratory also had longer dive times in the field. Short dive times of juvenile frogs may be associated with their transition from an aquatic to a terrestrial habitat. Reproductive activity was not associated with a prolonged dive time and therefore no particular breath holding capacities seem to be needed for egg laying. A submerged clasping male was not in any conflict situation between sustaining reproductive behaviour and physiological limitations to hold his breath.**

## INTRODUCTION

The diving behaviour of frogs has received little attention Large inter- and intraspecific variations in dive time may indicate that the decision to immerse and to surface depends on an individual's changing physiological and behavioural state, as well as on life-history aspects and particular external situations (HUTCHISON et al., 1976, PANDIAN & MARIAN, 1985, WEST & VAN VLIET, 1992) Individuals of many frog species spawn in water at a depth that requires complete submergence of the amplectant pair (EIBL-EIBESFELDT, 1956, DUELLMAN & TRUEB, 1985) and therefore interruption of breathing (ZUG, 1993). A clasping male, carried under water by the female and perhaps depending on her decision to surface, may enter a conflict between his first in priority activity, mating, and his second in priority activity, breathing,

Source : MNHN, Paris

similar to that of the male newt (HALLIDAY & SWEATMAN, 1976) Escaping from predators to an underwater shelter (SCHNEIDER, 1967), as well as diving behaviour involved in foraging activity (GANS, 1969) may also turn into a conflict situation. Thus, dives may be variable in duration because the animal's change in priority depends on several factors.

Reproductively active *Hyla labialis* stay in or near the ponds used for spawning, and dive when disturbed Non-reproductive adults as well as juveniles live an almost entirely terrestrial life away from water bodies (LÜDDECKE, 1995) and cannot avoid predators by diving Therefore, except when being reproductively active and spawning, individuals should show little tendency to dive To determine whether the tendency to dive, diving behaviour and dive time vary according to changes in habitat use and reproductive activity, we performed diving trials with recently metamorphosed juveniles and adult *H labialis* encountered during and between breeding seasons.

## MATERIALS AND METHODS

### STUDY ANIMALS

All experimental frogs came from 3500 m altitude in the Parque Nacional Natural Chingaza (4°42'N, 73°48'W) Details concerning the area and the collection technique were given elsewhere (LÜDDECKE, 1997). Between August 1996 and May 1997, frogs spent a week or less the laboratory. Frogs to be tested in the laboratory were selected in the field according to criteria related to their developmental stage and reproductive state. Snout-vent length was measured with a calliper to the nearest millimetre and body mass was determined with a laboratory balance to the nearest 0.1 g. We established six frog categories: (J) recently metamorphosed juveniles ($n$ = 19); (AM) reproductively active males encountered at the breeding pond and recognised by large and dark thumb pads, dark gular sac, heavy skin secretion and strong odor ($n$ = 15), (IM) reproductively inactive males, encountered far from the breeding pond, with small and pale thumb pads and pail throat ($n$ = 15), (GF) gravid females, with a body condition index of 80 or more (LÜDDECKE, 1995), oviducts or eggs often visible through the ventral skin ($n$ = 15), (SF) spent females, with a body condition index of 70 or less ($n$ = 15); and (P) amplectant pairs encountered in the breeding pond ($n$ = 5). AM and GF were usually found resting at the pond edge or in the water, whereas J, IM and SF were found away from the pond.

### EXPERIMENTAL PROCEDURE

Dive time measurements and behavioural observations were conducted in a glass aquarium 40 × 20 × 80 cm deep which had an internal jacket of plastic mesh 1 × 1 cm It was filled with unaerated water to 4 cm below the rim. Three controlled water temperatures were used, 8, 18 and 28°C, which are within the range of water temperatures in breeding ponds of *H labialis* (LÜDDECKE, 1995). The experimental temperature to be used was randomly determined for each of the three days (capture day and the following two days) when dive tests were

Source : MNHN, Paris

made. For a sequence of three days, each water temperature was used once. The assignment of frogs to temperatures was random. Preliminary tests had revealed no significant differences in dive time between frogs used on different days after capture.

In each dive test, a single individual was placed in a plastic tube at the experimental temperature during 30 min prior to a diving event, thus its body temperature equalled the experimental temperature when it was pushed from the tube into the tank at an angle of about 20 degrees to the water surface. This instant marked the beginning of a diving event. A diving event ended when the frog had returned to the water surface for breathing. Each individual was submitted at approximately 30-min intervals to three dive tests at the same temperature, carried out on the same evening between 18.00 and 21.00 h local time under artificial light.

Members of amplectant pairs were separated and male and female were first tested independently in the way described above, but only once. They were then allowed to clasp again, and the amplectant pair was tested once. However, in order to avoid accidental separation, the pair was not introduced into the tube and pushed into the water, but placed gently at the water surface of the tank from where it initiated the dive spontaneously.

Before being released at the capture site in the field, each unmated frog was submitted to one dive test in a natural pond. We placed it on a moss cushion at the pond edge, from where it would either jump into the water and dive immediately, or after being touched lightly on its back. Dive time and water temperature at the pond bottom were recorded.

### Behavioural observations

Diving frogs were observed continuously from the start to the end of each diving event and their behaviour recorded directly on a record sheet. According to preliminary observations, we distinguished three diving phases: descent, stationary phase and ascent. To describe diving behaviour we took into account the mode of locomotion, body postures, changes in head, body and leg position, and diving depth. As a measure of a submerged frog's activity we counted its moves. A move could be a small change in body posture, in the position of a leg, or a swimming stroke. In each phase we counted all occurrences. Total time of each diving event, and the duration of each diving phase, were determined with a stop watch.

### Statistical analysis

Dive time values of zero (frog did not dive) were excluded from analysis. All dive time values were $\log(x + 1)$ transformed in order to satisfy criteria for applying parametric tests (Zar, 1996). ANOVAs were used for comparisons between frog categories. Simple and multiple regressions were used to test for associations between temperature, dive time and moves. The comparison of field and laboratory dive times was made with a paired $t$ test. Data were processed using SYSTAT 5.2.1 for the Macintosh (SYSTAT Statistics, Evanston, Ill., Systat Inc.). A significance level of $P < 0.05$ was applied in all tests.

Source : MNHN, Paris

## RESULTS

### DIVING BEHAVIOUR

Most frogs dove in all three tests, except for one female and three juveniles. Another two juveniles refused to dive in two of the three tests, and four females, four males and two juveniles refused to dive in one test. Dive time was highly variable, the average for all events of all frog categories except amplectant pairs was 5.04 ± 6.06 min (range: 0.05-46.15 min, $n$ = 211), during which a frog made on average 46.6 ± 25.4 moves (range: 1-160 moves, $n$ = 199) at an average rate of 14.6 ± 10.9 (range: 1.5-82.7) moves per minute. Frogs dove to the tank bottom in 161 of 211 tests, in 50 tests they came to rest on the tank wall at various depths. At 28°C, we found no dive time difference between 29 tests where frogs came to rest on the tank wall, and 40 tests where they dove to the bottom (ANOVA; 1st event: $P$ = 0.19, $n$ = 24; 2nd event: $P$ = 0.69, $n$ = 24; 3rd event, $P$ = 0.08, $n$ = 21). The diving behaviour of amplectant pairs did not differ from that of unmated frogs. The clasping male seemed to play a passive role during the entire dive. None of the pairs spawned in the dive tank.

Most individuals (96 %) descended with powerful leg strokes while the arms were held backwards against the flanks. Few frogs descended by letting themselves sink. Some frogs initially sank and then swam toward the bottom. After making contact with the plastic mesh, the frog generally moved a short distance on the substrate before becoming stationary, the instant we took to be the end of the descent. On average, the descent took 0.08 ± 0.11 min (range: 0.03-0.96 min, $n$ = 89) or 1.6 % of total average dive time, and a frog made on average 25 % of its moves (mean = 10.9 ± 5.1, range: 1-28, $n$ = 174).

During the stationary phase, individuals remained at the same depth, most took a sitting or crouching posture and made occasional postural and limb movements and exceptionally short-distance moves. On average, this phase occupied 2.8 ± 2.9 min (range: 0.2-15.0 min, $n$ = 89) or 60.1 % of total average dive time, and contained 12.5 % of the moves (mean = 5.4 ± 8.9, range: 1-67, $n$ = 174).

The ascent began when the frog, still in a crouched posture, slightly lifted its head. The most common locomotory pattern was walking up the plastic mesh like on a ladder. Most individuals (93 %) ascended slowly by a sequence of alternating moves and halts. Some individuals actively swam to the surface and only a few let themselves float upward. There were also some cases of combining different locomotory patterns. The ascent ended when the frog's nostrils broke the water surface. On average, this phase took 1.8 ± 2.0 min (range: 0.08-10.5, $n$ = 71) or 38.4 % of total average dive time, and a frog made on average 62.5 % of its moves (mean = 27.3 ± 15.3, range: 1-144, $n$ = 174).

### COMPARISON OF SUCCESSIVE DIVING EVENTS OF AN INDIVIDUAL

All frog categories pooled, the first diving event (6.3 ± 7.9 min) was significantly longer than the second and the third (4.7 ± 4.9 min, 4.9 ± 5.4 min, respectively, repeated measures ANOVA, $df$ = 2, $P$ = 0.036). The difference became more pronounced after excluding juvenile frogs from the analysis (repeated measures ANOVA; $df$ = 2, $P$ = 0.019). The main reason was

Source : MNHN, Paris

that on average the first diving event of juvenile frogs was the shortest, whereas in the other frog categories the first diving event was the longest (GF, SF, AM and IM pooled; 1st event: 7.2 ± 8.5 min; 2nd event: 5.2 ± 5.2 min; 3rd event: 5.4 ± 5.7 min, for each category separately see tab. 1). We found no differences between the three diving events of all frog categories pooled, neither regarding the number of moves per dive (1st event: 50.9 ± 29.4, $n = 69$; 2nd event: 43.7 ± 22.2, $n = 67$; 3rd event: 44.9 ± 23.5, $n = 63$; ANOVA; $df = 2$, $P = 0.207$), nor the move rate (1st event: 15.7 ± 12.6, $n = 69$, 2nd event: 14.9 ± 11.7, $n = 67$; 3rd event: 13.1 ± 7.9, $n = 63$; ANOVA; $df = 2$, $P = 0.395$).

### Comparison among categories and gender

There were significant dive time differences among frog categories (ANOVAs, all events pooled: $df = 4$, $P = 0.0001$; 1st event: $df = 4$, $P = 0.029$, $n = 58$, 2nd event: $df = 4$, $P = 0.167$, $n = 57$; 3rd event: $df = 4$, $P = 0.017$, $n = 54$), due to juveniles having shorter dive times than adults. After excluding juveniles from analysis, no differences remained between categories (ANOVA; $df = 3$, $P = 0.246$). Thus, although gravid females and reproductively active males tended to dive less time than spent females and reproductively inactive males in almost all diving events at all temperatures, adult males and females had statistically indistinguishable dive times (ANOVAs; all events: $df = 3$, $P = 0.724$, 1st event: $df = 3$, $P = 0.69$, $n = 58$; 2nd event: $df = 3$, $P = 0.29$, $n = 57$, 3rd event: $df = 3$, $P = 0.31$, $n = 54$). We found no differences among frog categories regarding the number of moves during the dive (ANOVA; $df = 4$, $P = 0.841$), but significant differences in move rate (ANOVA; $df = 4$, $P = 0.015$), because juveniles had higher rates due to their shorter dive times (tab. 2).

Dive time of amplectant pairs (mean = 6.4 ± 5.2 min, range: 2.4-15.3 min), only measured at the intermediate temperature, did not differ significantly from that in any event of all unmated adult frog categories at that temperature (ANOVAs; $df = 4$ and $n = 43$ in all cases, 1st event: $P = 0.903$; 2nd event: $P = 0.366$, 3rd event: $P = 0.858$). When clasped by a male, the female tended to dive insignificantly longer than when diving by herself (mean = 5.4 ± 3.2 min, range: 1.0-9.5 min; paired $t$ test, $t = 0.33$, $P = 0.759$). The male of mated pairs, diving by himself, had an insignificantly shorter dive time (mean = 1.7 ± 0.5 min, range: 1.2-2.4 min) than the female diving by herself (paired, two-tailed $t$ test, $t = 2.29$, $P = 0.084$), and a marginally significant shorter dive time than when being taken under water by the female he was clasping (paired, two-tailed $t$ test, $t = 2.53$, $P = 0.064$).

### Relationships between dive time, moves, and temperature

The longer the dive, the more moves did a frog make (fig. 1a). Multiple regression analysis shows that the number of moves was related to dive time (*Beta* coefficient = 0.41, $P = 0.0001$), but not to temperature (*Beta* coefficient = 0.04, $P = 0.388$, fig. 2a). Since the number of moves was similar at different temperatures, but average total dive time shortened at higher temperatures (linear correlation coefficient, $r = 0.46$, $P = 0.0001$, fig. 2b), short dives had very high move rates (fig. 1b). Multiple regression analysis indicates that both, move rate and temperature (fig. 2c), significantly affect dive time (*Beta* coefficients; move rate: -0.515, $P = 0.0001$, $n = 199$, temperature: 0.346, $P = 0.001$). The positive relation between moves and

Source : MNHN, Paris

Table 1. – Dive time comparison of 75 *Hyla labialis* belonging to five categories, each individual tested three times (events 1, 2, 3) at one of three temperatures. (J) juvenile frogs; (IM) reproductively inactive males; (AM) reproductively active males, (SF) spent females; (GF) gravid females. Sample size (in brackets) refers to number of individuals.

| Temperature | Event | J | IM | AM | SF | GF |
|---|---|---|---|---|---|---|
| 8°C | 1 | 5.1 ± 6.8 (5) | 12.4 ± 13.6 (5) | 7.4 ± 3.6 (5) | 14.0 ± 18.2 (5) | 9.8 ± 4.8 (5) |
| | 2 | 5.8 ± 4.8 (4) | 7.1 ± 6.1 (5) | 4.6 ± 1.9 (5) | 13.2 ± 11.1 (5) | 6.5 ± 2.6 (4) |
| | 3 | 2.2 ± 4.1 (4) | 5.2 ± 2.4 (5) | 6.6 ± 3.6 (5) | 18.4 ± 12.7 (4) | 4.8 ± 2.2 (5) |
| 18°C | 1 | 2.1 ± 1.5 (5) | 7.8 ± 5.2 (5) | 9.8 ± 11.9 (4) | 4.3 ± 2.1 (4) | 3.7 ± 1.8 (5) |
| | 2 | 2.1 ± 1.3 (5) | 6.8 ± 5.1 (5) | 3.5 ± 2.8 (5) | 4.5 ± 2.4 (4) | 3.7 ± 1.9 (5) |
| | 3 | 3.7 ± 3.1 (5) | 6.9 ± 4.9 (5) | 5.2 ± 2.4 (5) | 3.1 ± 2.9 (4) | 4.2 ± 1.7 (5) |
| 28°C | 1 | 1.3 ± 0.6 (4) | 2.1 ± 1.7 (5) | 2.7 ± 1.1 (5) | 4.9 ± 4.1 (5) | 1.4 ± 0.7 (5) |
| | 2 | 1.7 ± 1.7 (5) | 1.8 ± 1.7 (5) | 1.9 ± 1.6 (5) | 2.5 ± 1.3 (5) | 1.8 ± 0.4 (4) |
| | 3 | 1.5 ± 1.6 (5) | 2.5 ± 0.6 (3) | 2.4 ± 0.8 (4) | 1.9 ± 0.7 (4) | 1.4 ± 0.5 (5) |
| All temperatures | 1 | 2.4 ± 3.6 (12) | 8.4 ± 9.3 (13) | 6.7 ± 6.9 (13) | 8.9 ± 12.0 (12) | 4.8 ± 4.5 (13) |
| | 2 | 2.6 ± 2.4 (12) | 5.9 ± 5.0 (13) | 3.3 ± 2.4 (13) | 7.7 ± 8.4 (12) | 3.9 ± 2.6 (13) |
| | 3 | 2.8 ± 3.0 (12) | 5.2 ± 3.6 (13) | 4.9 ± 3.1 (13) | 7.8 ± 10.4 (12) | 3.6 ± 2.2 (13) |

Table 2 – Dive time and activity comparisons of 75 *Hyla labialis* belonging to five categories, including all three events and all three temperatures (J) juvenile frogs; (IM) reproductively inactive males; (AM) reproductively active males, (SF) spent females; (GF) gravid females. Sample size refers to the number of dives.

| Frog category | *n* | Dive time (min) | Number of moves | Moves per minute |
|---|---|---|---|---|
| J | 31 | 3.7 ± 3.6 | 45.7 ± 28.3 | 19.1 ± 14.9 |
| IM | 43 | 6.0 ± 6.3 | 46.8 ± 28.1 | 12.7 ± 9.1 |
| AM | 43 | 4.8 ± 4.5 | 50.4 ± 28.6 | 15.0 ± 11.7 |
| SF | 39 | 7.7 ± 9.8 | 45.7 ± 25.9 | 10.8 ± 7.8 |
| GF | 43 | 4.1 ± 3.3 | 44.2 ± 15.4 | 16.2 ± 10.1 |

dive time is mainly due to the ascent, which contained 62.5 % of the moves, and less to the descent and the stationary phase, which contained only 25 % and 12.5 %, respectively, of the total number of moves.

### FIELD OBSERVATIONS

None of the frogs tested in the field tried to escape by moving away from the pond. All frogs dove to the bottom of the pond and usually entered the soft layer of mud where they were invisible to observers. They reappeared at the beginning of the ascent, when they lifted their head out of the mud, usually close to where they had entered. They remained for up to several minutes in this position, before they continued the ascent by leaving the mud and

Source : MNHN, Paris

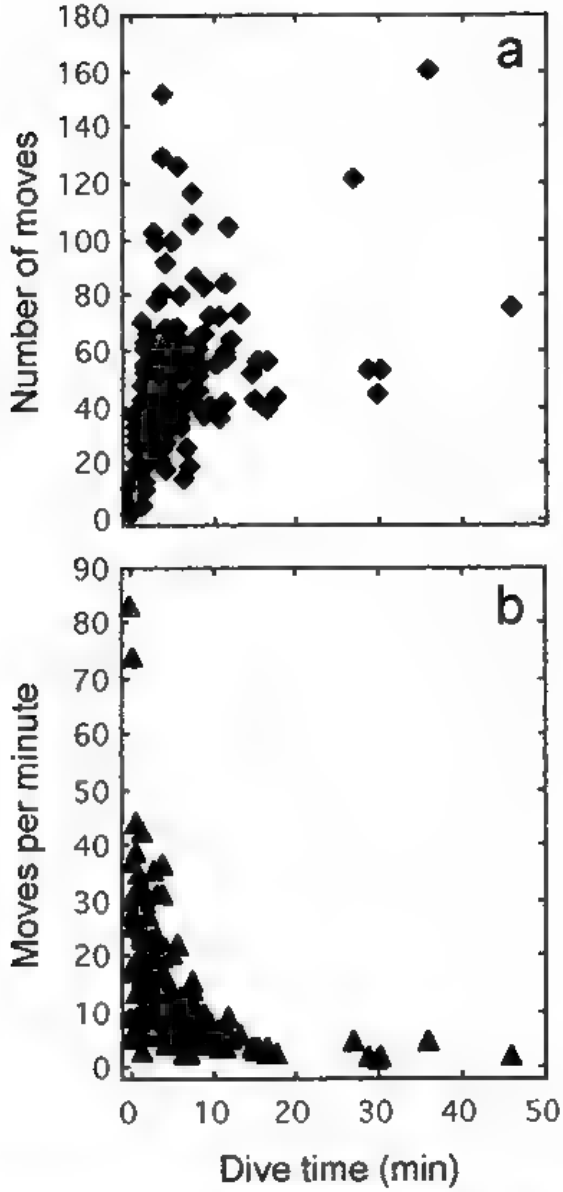


Fig. 1 Relationships between dive time in the laboratory, number of moves during a dive, and rate of moves, in *Hyla labialis* All events included

swimming to the surface, or by first walking some distance on the mud surface and then slowly climbing up aquatic plants.

There were no significant field dive time differences among frog categories (ANOVA, $df = 4$, $P = 0.069$), even though juvenile frogs had rather short, and reproductively inactive males had rather long dive times. Pooled dive times for all categories at corresponding temperatures (using the laboratory record for low or intermediate temperatures closest to the temperature of each frog diving in the field) were significantly longer in the field (8 9 ± 6 6 min) than in the laboratory (6 5 ± 5 8 min, two-tailed paired $t$ test, $df = 37$, $t = 3\ 27$, $P = 0\ 002$) Individual field and laboratory dive times were significantly and positively correlated for all individuals (linear correlation coefficient, $r = 0.74$, $P = 0.0001$, $n = 37$), and also within each of three (SF, AM, J) of five categories (fig 3)

Source : MNHN, Paris

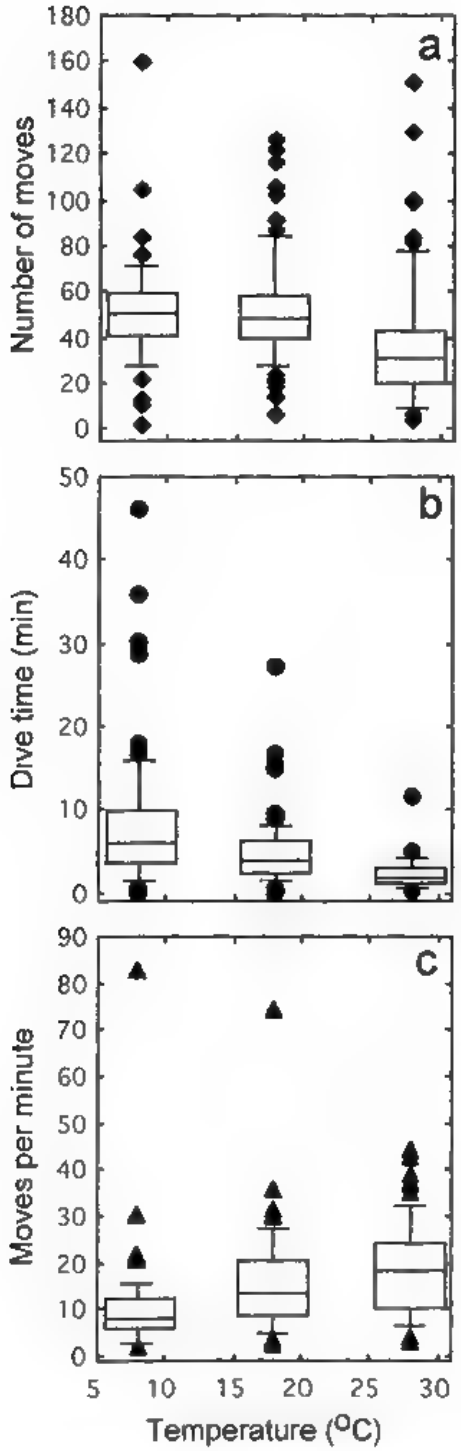


Fig 2 Relationships between water temperature dive time in the laboratory number of moves during a dive, and rate of moves, in *Hyla labialis* All events included

Source : MNHN, Paris

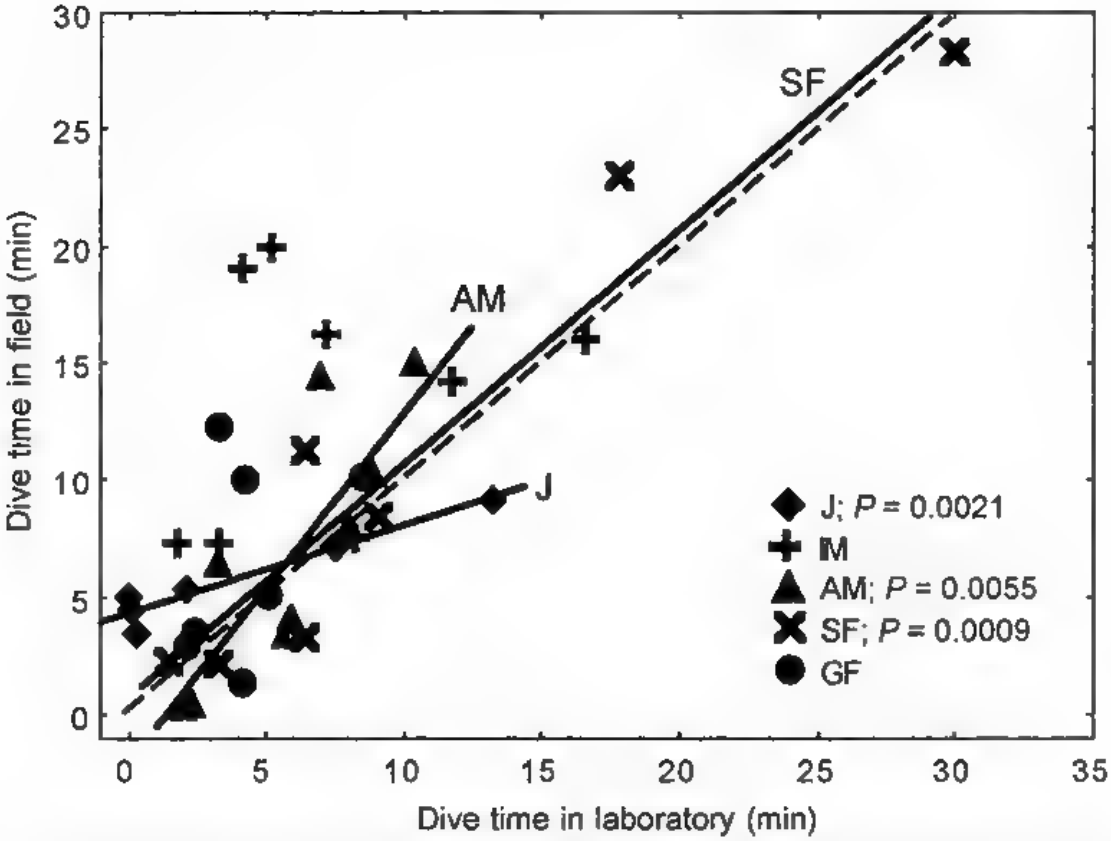


Fig 3 Relationship between dive times in the laboratory at 8 or 18°C, and in a natural pond at 9-16°C, of 37 *Hyla labialis* belonging to five frog categories. Diagonal traced line indicates dive times of equal duration. Continuous lines are regression lines for three frog categories.

## Discussion

Since frogs sun basking on a moss cushion at the pond edge plunged into the water when disturbed, diving was assumed to be a protective behaviour against terrestrial predators. In this context, the function of the descent is to take the frog down fast and efficiently by actively swimming towards the bottom. The relatively long lasting and passive stationary phase also indicates that a frog dives to escape, particularly since in a natural pond the diver usually penetrates into the mud layer at the bottom of the pond, where it is visually concealed. Finally, lifting the head and looking upward before beginning to ascend, as well as the frequent halts of the frog on its way up, could be interpreted as vigilance by visually screening the surroundings for predators across the totally transparent water of these natural ponds. According to our procedure, we assumed that the frogs would perceive the push into the water as a predator attack, and expected dive time and behaviour to be related to the risk. If risk were related to body size, then juvenile frogs should dive longest. This expectation was not fulfilled. Alternatively, since a frog probably ignores a predator's persistance in waiting for it to surface, its antipredator strategy may as well be to surface at an unpredictable moment

Source : MNHN, Paris

(BAIRD, 1983). Further, despite the difference in procedure, amplectant pairs showed the same behavioural diving patterns and similar dive times as did unmated frogs, which suggests that the predator-simulating push did not have much influence on dive time.

The high variability of dive times suggests that changes in behavioural priorities are involved (HALLIDAY & SWEATMAN, 1976). For instance, juvenile *H. labialis* are in transition to a terrestrial lifestyle, thus the lower tendency to dive and shorter dive times of metamorphosed frogs may be associated with avoidance of a high predator risk in the aquatic habitat (WILBUR & COLLINS, 1973; WASSERSUG & SPERRY, 1977; SKELLY, 1994). Reproductively active frogs may terminate a dive in order to continue mate searching, which is done at the water surface. The exceptionally short dive times of males of pairs, diving by themselves after having been separated from the female, may reveal restlessness motivated by searching for the missing mate.

The rather paused return to the surface suggests that *H. labialis* begin to ascend long before depleting their oxygen stores. Although an urge to breathe is unlikely to be second in priority, physiological aspects may play a role in diving behaviour. For instance, the negative correlation between underwater activity and dive time of *H. labialis*, also found in other amphibians (HALLIDAY & WORSNOP, 1977), is associated with temperature, and together they may determine when threshold levels of blood oxygen concentration are reached (HUTCHISON et al., 1976; BOUTILIER, 1990). Since unmated males had dive times similar to those of pairs, we assume that a male clasped to a submerged female is not in any conflict between holding on to her or breathing. Apparently, spawning behaviour does not rely on particular breath holding capacities, because the time spent submerged for spawning seems to be very short in most anuran species (see WEYGOLDT & POTSCH, 1992). The tendency to dive may also be associated with temperature preferences or individual experiences. Although *H. labialis* is thermophilic (VALDIVIESO & TAMSITT, 1974; LÜDDECKE, 1995), the unfamiliar experience to descend into a warm depth may be the reason for a reduced tendency to dive to the bottom of the tank at high water temperatures, since in nature it would always find cooler temperatures as it dives deeper. Finally, since an individual frog tended to make either longer or shorter dives, irrespective of place and time of day, performance differences among individuals may be due to inherent physiological or behavioural properties.

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Source : MNHN, Paris

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# On distribution of and hybridisation between the newts *Triturus vulgaris* and *T. montandoni* in western Ukraine

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**A case of natural hybridisation between the newts *Triturus vulgaris* and *T. montandoni* was recorded in the Maloye Opolie area, Lvov province, western Ukraine, where the latter species is represented by a population geographically isolated from the main range in the Carpathian mountains. A female hybrid, probably of the first generation, was identified by means of DNA flow cytometry. No hybrids were found in the Ukrainian Carpathians. Syntopic occurrence of *T. montandoni* and *T. vulgaris* in western Ukraine is discussed.**

## INTRODUCTION

The Montandon's newt, *Triturus montandoni* (Boulenger, 1880), is endemic to the Carpathian mountains. The species occurs in the Ukrainian Carpathians from 150 up to 2000 m above sea level (SZCZERBAK & SZCZERBAN, 1980). The range of *T. montandoni* is wholly surrounded by the range of *T. vulgaris*. However, both ranges are, in fact, parapatric. Nevertheless, the two species can coexist in the same water body. Such cases of syntopic occurrence have been reported in Romania (FUHN, 1963, ŞOVA, 1973, FUHN et al., 1976, our data), Slovakia (GULIČKA, 1954), Czech Republic (REHÁK, 1993), Poland (SZYMURA, 1974, JUSZCZYK, 1987) and in Ukraine (HORBULEWICZ, 1927, SZCZERBAK & SZCZERBAN, 1980, fig.1).

*Triturus montandoni* is genetically closely related to *T. vulgaris*, and both species have similar sexual behaviours (BELYAEV, 1979, 1981, PECIO & RAFINSKI, 1985; RAFINSKI & ARNTZEN, 1987; ARNTZEN & SPARREBOOM, 1989). Therefore, it is not surprising that in the laboratory the two species can hybridise and that such crosses can provide fertile adult offspring (WOLTERSTORFF, 1925; GEYER, 1953 cited from FUHN, 1963, MACGREGOR et al., 1990; COGĂLNICEANU, 1994; our data).

Source : MNHN, Paris

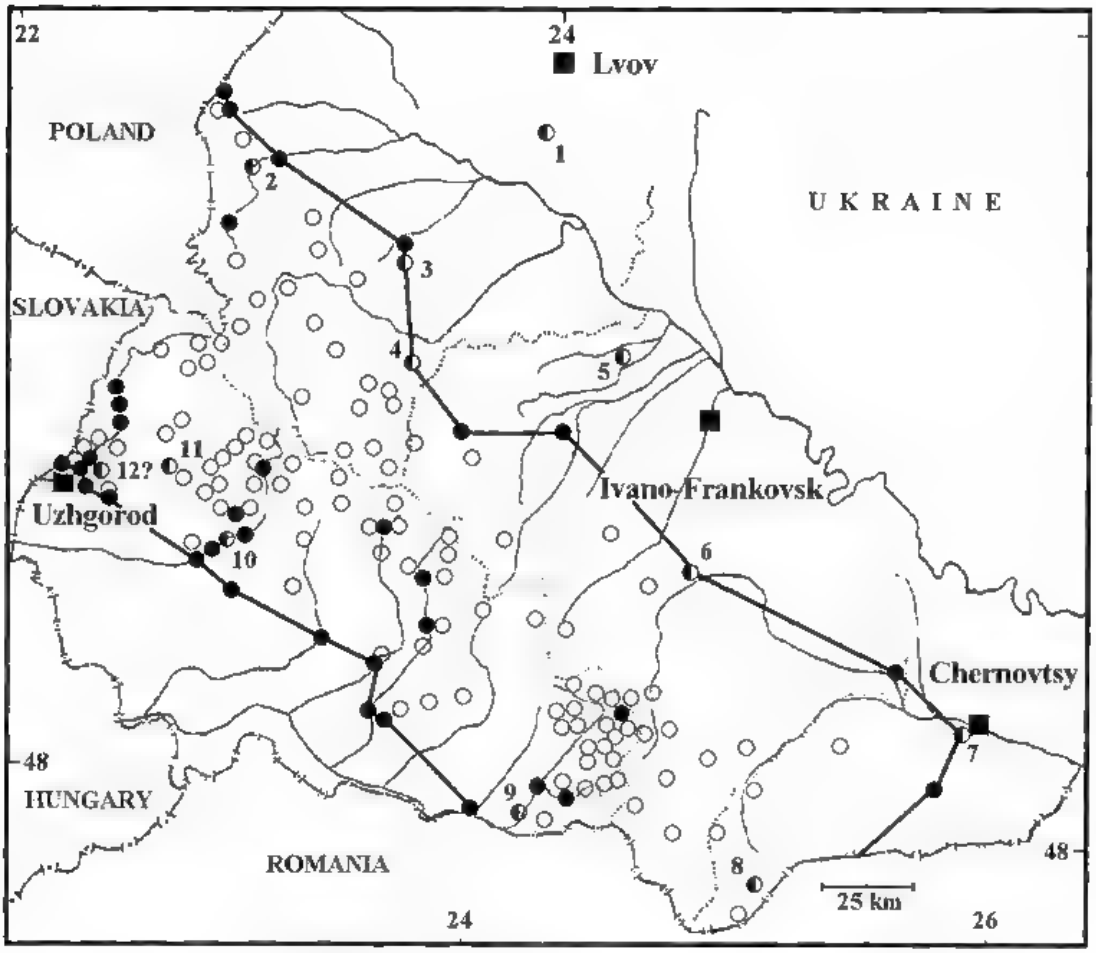


Fig. 1. Distribution of *Triturus montandoni* (open circles) in western Ukraine. The localities shared with *T. vulgaris* (semiopen circles) are: (1) Rakovets, 295-350 m; (2) Stary Sambor, 709 m; (3) Truskavets, 300-360 m; (4) Skole, 430 m; (5) Vorulov, 350 m; (6) Delyatin, 500 m; (7) Chernovtsy, 150-250 m; (8) Dolishny Shepot; (9) Delovoe, 365 m; (10) the Karpaty sanatorium, 165 m; (11) Poroshkovo; (12) Domanintsy. (13) Kriva. Sources: (1), (3) & (13), our data; (2) HOFMANN (1908); (3) POLUSHINA & KUSHNIRUK (1962); (4-8) & (11), SZCZERBAK & SZCZERBAN (1980); (9) O. A. Lugovoy & V. F. Pokinchereda (pers. comm.); (10) N. L. Orlov (pers. comm., ZMM 1404 & 2975, ZISP 5025, 5026 & 5561); (12) KUSHNIRUK (1963). Solid circles are sporadic localities of *T. vulgaris* in the Carpathians. The border of the main distribution of *T. vulgaris*, beyond the mountains, is marked by a black line.

In the breeding period, male hybrids obtained from laboratory crosses have a combination of various features: from *T. montandoni* - long tail filament (4 mm), well-developed dorsolateral ridges, black feet, gray throat without spots and bright orange belly, and from *T. vulgaris* - dorsal crest (height 1.5 mm) and small black dots on the belly. Female hybrids differ slightly from females of *T. montandoni*, although hybrids have small black spots on the belly.

In the field, several authors found newts with a pattern similar to that of the laboratory hybrids and recognized them as natural hybrids. For instance, such newts were reported from

Source : MNHN, Paris

western Ukraine (fig. 1: localities 2, 3 and 12), Romania (FUHN, 1963; FUHN et al., 1976) and Czech Republic (REHÁK, 1993). However, such records are uncommon, and in Slovakia, for instance, long term (16 years) observations on syntopic populations of *T. montandoni* and *T. vulgaris* provided no hybrids (GULIČKA, 1953).

An application of biochemical techniques could facilitate more reliable identification of such presumptive hybrids, based on external characters only. We know only two cases where interspecific hybridisation has been confirmed by allozyme analysis. In some syntopic localities in Poland, the incidence of hybrids, which were mainly recombinants, varied between four and 60 % (PLEIO & RAFINSKI, 1985, RAFINSKI, 1985). In a Czech locality where both species coexisted, five specimens with intermediate characters were collected (KOTLÍK et al., 1997). Based on three loci, four animals were identified as hybrids: one individual, perhaps, was a product of a backcross of the second generation and others were the offspring of more distant crosses. No hybrids of the first generation were found.

*Triturus montandoni* is protected in many countries. The species is listed in the Red Data Book of Ukraine although its local density can be quite high. Based on our data, *T. montandoni* is very common and obviously predominates over any other newt species in the Ukrainian Carpathians. COGĂLNICEANU (1997) suggested that, although not sufficiently documented, hybridisation with *T. vulgaris* may contribute to the reduction of its range and even pose a threat to its long term conservation.

The goal of our study was to investigate possible hybridisation between *T. montandoni* and *T. vulgaris* in western Ukraine.

## MATERIALS AND METHODS

In 1989-1996 we searched for presumed hybrids between *T. montandoni* and *T. vulgaris* in all districts of Zakarpatskaya Province, as well as in Turka, Sambor, Khyrov, Drogobych, Nikolaev and Pustomyty districts of Lvov Province. In total we examined, mainly in the field, the external characters of above one thousand individuals of *T. montandoni* and *T. vulgaris* from western Ukraine including 567 individuals from the Maloye Opolie area (tab. 1). After careful examination, the animals were usually released to the same water body where they had been collected. Some animals, including 27 individuals from Maloye Opolie, were studied by DNA flow cytometry.

The amount of DNA per nucleus (genome size) was determined in relative units as a ratio of the fluorescence intensity of cells from an individual examined to that of reference cells. The details of the technique have been published by VINOGRADOV et al. (1990). Peripheral blood cells of *Pleurodeles waltl* were used as a standard.

Apart from our field study, we examined some museum collections. Museum abbreviations are: IZK, Institute of Zoology, Ukrainian Academy of Sciences, Kiev, Ukraine; ZISP, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia; ZMM, Zoological Museum, Moscow State University, Moscow, Russia.

Source : MNHN, Paris

Table 1. – Occurrence of four newt species along the Rakovets gradients from the forest edge to the deep forest. Abbreviations: *T. m.*, *Triturus montandoni*, *T. v.*, *T. vulgaris*; *T. a.*, *T. alpestris*; *T. c.*, *T. cristatus*.

| Waterbodies | | Forest edge | | | | 600-700 m from the forest edge | | | | 2200-3000 m from forest edge | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Newt species | | *T. m.* | *T. v.* | *T. a.* | *T. c.* | *T. m.* | *T. v.* | *T. a.* | *T. c.* | *T. m.* | *T. v.* | *T. a.* | *T. c.* |
| Date: | 29.05.94 | no data | | | | 123 | 3 | 19 | 3 | no data | | | |
| | 18.04.95 | 0 | 2 | 0 | 0 | 186 | 0 | 10 | 10 | no data | | | |
| | 11.05.96 | 2 | 0 | 0 | 0 | 144 | 0 | 23 | 2 | 102 | 0 | 35 | 0 |

Table 2. – Genome size variation in *Triturus vulgaris* and *T. montandoni*.

| Province | *n* | Mean | Standard deviation | Range |
|---|---|---|---|---|
| *T. vulgaris* | | | | |
| St. Petersburg | 77 | 1.121 | 0.011 | 1.076-1.147 |
| Zakarpatskaya | 75 | 1.120 | 0.011 | 1.089-1.144 |
| Lvov | 7 | 1.111 | 0.011 | 1.096-1.127 |
| *T. vulgaris* × *T. montandoni* | | | | |
| Lvov | 1 | – | – | 1.150 |
| *T. montandoni* | | | | |
| Lvov | 19 | 1.182 | 0.009 | 1.167-1.199 |
| Zakarpatskaya | 6 | 1.176 | 0.011 | 1.158-1.189 |

## Results and discussion

Having checked the zone of parapatry of *T. montandoni* and *T. vulgaris*, we found that some localities (fig. 1: 9 and 10) were inhabited by either of the two species only, although previous authors listed both species there. No morphological hybrids were identified.

On June 9, 1990, a sole locality with syntopic *T. montandoni* and *T. vulgaris* was recorded in the surroundings of Truskavets, Lvov province, near the town's water reservoir (fig. 1: locality 3). In a small round puddle (diameter 3 m, depth 15 cm) situated in an depression on the ground road nearby the forest, six individuals of *T. vulgaris* (3 males and 3 females) and a female of *T. montandoni* were found. Despite our attempts, no males of *T. montandoni* were observed there. Curiously, the only female of the latter species was transferred to St.

Source : MNHN, Paris

Petersburg and laid eggs successfully. Normal larvae hatched and metamorphosed The juveniles had unspotted bellies and were similar to those of *T. montandoni* Later these animals died for various technical reasons. Unfortunately, we failed to identify the presumptive hybrid origin of these young individuals.

In 1994-1996, our special attention was focused on an isolated population of *T. montandoni* from the surroundings of the village Rakovets, Pustomyty district, Lvov province, which is situated 30 km south of Lvov city (fig 1: locality 1). This hilly area named Maloe Opolie is recognized by geographers as an extension of the Bobrko-Stolskoye Kholmogorie which belongs to the Podolskaya eminence. The area is partly covered by a small beech forest of the so-called Carpathian type which is separated from the beech forests of the Carpathian mountains by the valley of Dniester river over a distance above 50 air kilometers. This isolation seemed to be associated with changes in the Carpathian forest limits in the Atlantic epoch, i.e. 5-8 thousand years ago (MALINOVSKY, 1991).

This area is inhabited by all four newt species which are distributed in the Carpathian mountains, i.e., *T. vulgaris*, *T. cristatus*, *T. alpestris* and *T. montandoni*. The two latter species are obviously represented by populations geographically isolated from their main ranges in the Carpathians. BAYGER (1937, 1959) was the first to publish local records of *T. montandoni* and *T. alpestris*. He listed 38 localities covering the Maloye Opolie area as a whole (BAYGER, 1938 cited from GULIČKA, 1954). Surprisingly, later in soviet time these Bayger's papers were forgotten, and the locality labels of his Opolie specimens kept in the Ukrainian museums of natural history in Kiev (e.g., a jar with the Rakovets sample of *T. montandoni*, IZK 80) and in Lvov (TARASHCHUK, 1959) were considered to be incorrect! However, relatively recently (in 1985), some localities mentioned by Bayger were repeatedly discovered by local researchers (S.V. Shaytan, pers. com cited from TATARINOV, 1989; POLUSHINA et al., 1989).

In 1994-1996, we monitored distribution of both species in Maloye Opolie along a gradient from the forest edge to deep forest which coincided with a gap arranged by forest cutting and used by forest trucks. Three sites were observed

(1) The first one was situated on the military site nearby the forest edge (295 m above sea level) There were few water bodies (ditches, total length 10 m, width about 1 m, depth 0.5 m) with dense water vegetation and mosses. These water bodies were visited in 1995 and 1996: during our first visit only *T. vulgaris* was found, whereas in the second visit we observed both species and captured only *T. montandoni* (tab. 1). The densities of the two species were quite low

(2) The second site was situated in the forest, 600-700 m from the edge, on a slope of a small hill (350 m above sea level). Here in 1994, in wheel-tracks filled by water, we found four newt species (tab. 1), with a predominance of *T. montandoni* The latter species was characterized by high density: for instance, 123 individuals were collected in a wheel-track (length 25 m, width 0.6 m, depth 0.4 m). However, *T. vulgaris* was quite rare (two males and one female only) In 1994, we also captured a female which had some external features similar to those of *T. montandoni*, and black spots on the belly like in *T. vulgaris* The study by flow DNA cytometry established that this female had a genome size (tab. 2) intermediate between those of both species. Interestingly, the lab hybrids of the first generation, obtained by us in the cross of a male *T. vulgaris* and a female *T. montandoni*, had a similar genome size Therefore, we incline to identify this "morphological hybrid" female as a true first generation hybrid

Source : MNHN, Paris

between both species. The study of the second water body was continued in 1995 and 1996. However, we failed to find either *T. vulgaris* or new hybrids (tab. 1).

(3) The third site (350 m above sea level) was also situated in a wheel-track in deep forest, 2200-3000 m from the edge. We visited the water body in 1996 only and found only *T. montandoni* and *T. alpestris*. The former species was represented by some unusual individuals, e.g. by a female with a shortened body or by other animals (1.5 % of the Maloye Opolie sample) with partial or total lacks of black or orange pigmentation. However, such abnormalities in local animals seemed to have no association with any hybridisation between *T. montandoni* and *T. vulgaris*, because we found similar colour abnormalities in *T. alpestris* as well, with an incidence up to 2.3 %. In contrast, we observed no abnormal individuals of these species in the Carpathian mountains. We suggest that the appearance of such abnormalities may be explained by peculiarities of the isolated newt populations of Maloye Opolie.

Consequently, despite the "enclave" status of *T. montandoni* in the Maloye Opolie area, the local contact zone between this species and *T. vulgaris* seems to be very narrow. Only few individuals of the latter species penetrated into the forest water bodies predominantly inhabited by *T. montandoni*. RAFINSKI (1985) reported that in Poland hybrid individuals were more common in populations where *T. vulgaris* was more abundant rather than in populations with predominating *T. montandoni*. Our finding is in agreement with this observation because the sole Maloye Opolie hybrid was found in the site with very sparse presence of *T. vulgaris*.

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Source : MNHN, Paris

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